Issued June 18, 1910.

U. S. DEPARTMENT OF AGRICULTURE,

FOREST SERVICE—BULLETIN 79.

HENRY S. GRAVES, Forester.

THE LIFE HISTORY OF LODGEPOLE BURN FORESTS.

BY

F. E. CLEMENTS,

Collaborator.

WASHINGTON:
GOVERNMENT PRINTING OFFICE.
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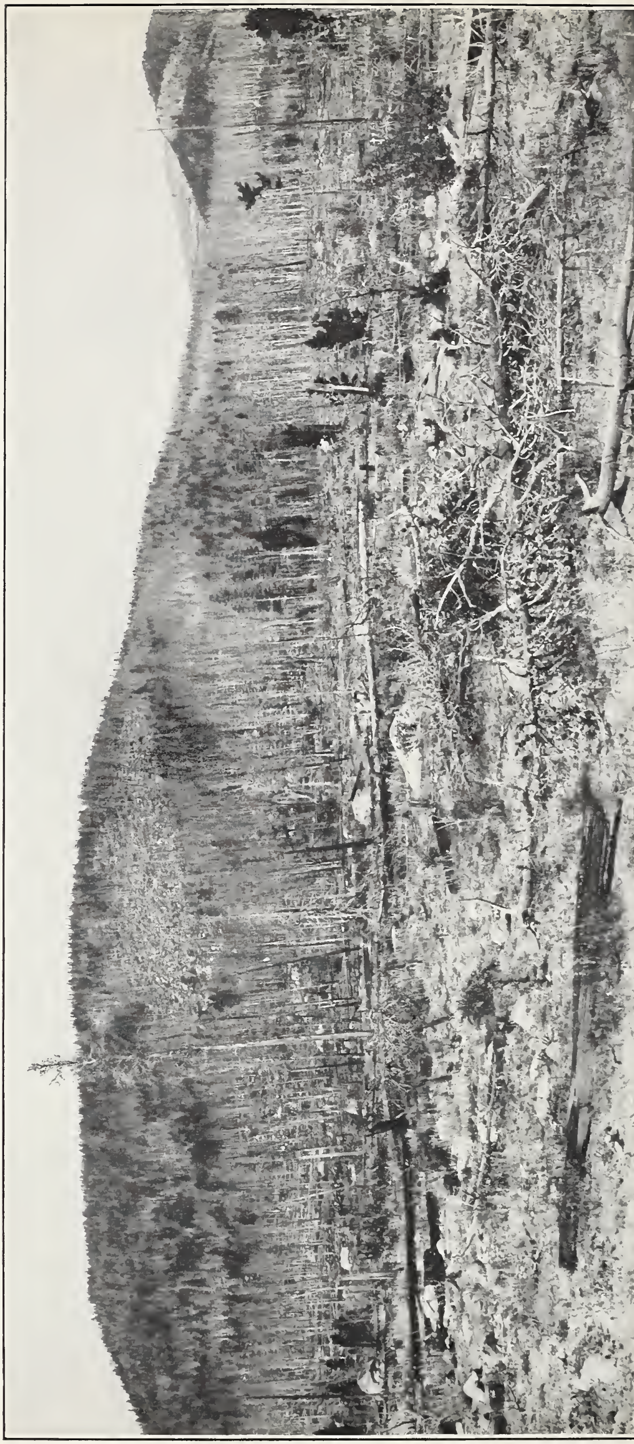

BURN OF 1901 ON MORAINE RIDGE.

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LETTER OF TRANSMITTAL.

U. S. DEPARTMENT OF AGRICULTURE,
FOREST SERVICE,
Washington, D. C., January 15, 1910.

SIR: I have the honor to transmit herewith a report entitled "The Life History of Lodgepole Burn Forests," by F. E. Clements, Collaborator, and to recommend its publication as Bulletin 79 of the Forest Service. The six plates and text figure accompanying the manuscript are necessary for its proper illustration.

Very respectfully,

ALBERT F. POTTER,
Acting Forester.

HON. JAMES WILSON,
Secretary of Agriculture.

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THE LIFE HISTORY OF LODGEPOLE BURN FORESTS.[a]

THE FORESTS OF ESTES PARK.

As a typical forest area of northern Colorado, Estes Park is an apt field for study. Its forests show the zonation of species typical of northern Colorado, and the numerous fires which have occurred at intervals of a number of years give an opportunity for the study of the life history of the burned areas. In this park the open grassland areas are merely upward extensions of the Bouteloua or shortgrass formation of the Great Plains to altitudes of from 7,500 to 8,500 feet. From 8,500 to 9,000 feet the grass land is represented by typical mountain meadows. The oak-cercocarpus thicket and the juniper-piñon woodland of the foothills, one or both of which usually form a characteristic zone between the plains and the mountain forests, do not exist in the park. Cercocarpus forms a typical thicket on the foothills which border the eastern wall, but as a type it disappears as the higher levels toward the park are reached, and, like juniper, is then found only as scattered individuals. Along the western wall the thicket has also disappeared, and the invading sagebrush not only touches the yellow-pine woodland, but is its characteristic undergrowth.

The forest of Estes Park shows fairly well-defined types: (1) The yellow-pine type, (2) the lodgepole-Douglas fir type, and (3) the Engelmann spruce-alpine fir type. The yellow-pine type is typically an open woodland, reaching from the upper foothills to an altitude of 9,000 feet. In the canyons and on the higher slopes it is mixed with Douglas fir and lodgepole, and finally gives way to them. Yellow pine occupies the ridges and slopes of the lower park, whence it extends downward to the small knolls scattered through the open. At higher elevations it necessarily occurs only in the open valleys. In the open park it occupies small rocky knolls and ridges, from which it invades the grass land proper. The lodgepole and the Douglas fir are essentially cozonal, though the former reaches higher altitudes and the latter lower. The Douglas fir occupies a zone be-

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[a] The writer acknowledges with gratitude the invaluable assistance of Dr. Edith Clements and Prof. Albert T. Bell during the summers of 1907 and 1908 and of Mr. Raymond J. Pool during the summer of 1907.

tween yellow pine and Engelmann spruce, but it has been so largely replaced by lodgepole pine, as a result of fires, that pure stands are rare. This central zone begins at about 8,000 feet and extends up to 10,000 feet. As a rule it yields to the third zone of forest before timber line is reached. When the Engelmann spruce and alpine fir have been destroyed by fire, however, dwarfed lodgepole pine, for the time at least, forms the timber line itself. The last zone, consisting of Engelmann spruce, alpine fir, and limber pine, is often poorly defined and very narrow, but it regularly forms the forest at timber line and for some distance below. The three species rarely meet on equal terms. Limber pine is more abundant at lower altitudes, sometimes forming nearly pure stands at from 9,500 to 10,000 feet. Its altitudinal range, however, is unusual, for it occurs with yellow pine in the open park at 7,800 feet, and it also takes its place in the forest frontier at 10,500 feet on Longs Peak. In the heavy forest below timber line Engelmann spruce and alpine fir often meet upon fairly equal terms. Both push well down into the lodgepole belt, and outposts are carried down along the streams to 8,500 or even 8,000 feet.

Of the other trees in the park, juniper does not here form forests, and blue spruce does so but rarely. The juniper occurs only in the lower park. Blue spruce grows either isolated or in small clumps, along the streams, up to an altitude of 8,500 feet. Although most abundant in the lodgepole type, aspen occurs throughout the three types, reaching its best development along the streams, where the alder associates with it in small numbers. In Estes Park aspen rarely reaches either the abundance or importance it attains where lodgepole is lacking. As pioneer trees in burns, it is almost inevitable that one or the other should have the advantage. The causes and significance of this relation will be considered later.

BURNS IN ESTES PARK.

The study of burns in the park indicates an extraordinary succession of fires, encountered nowhere else in Colorado. This is due to features of climate and topography both directly and indirectly favorable to fires. Temperature records show that Estes Park is warmer than similar altitudes much farther south in the mountains. It must have been for centuries a favorite region of the Indians during the summer. It was also early entered and settled by white men. These facts are perhaps sufficiently self-explanatory. It is probably unjust, however, to attribute all the fires to man. During two summers' work nearly a dozen fires were noted which were due to lightning.

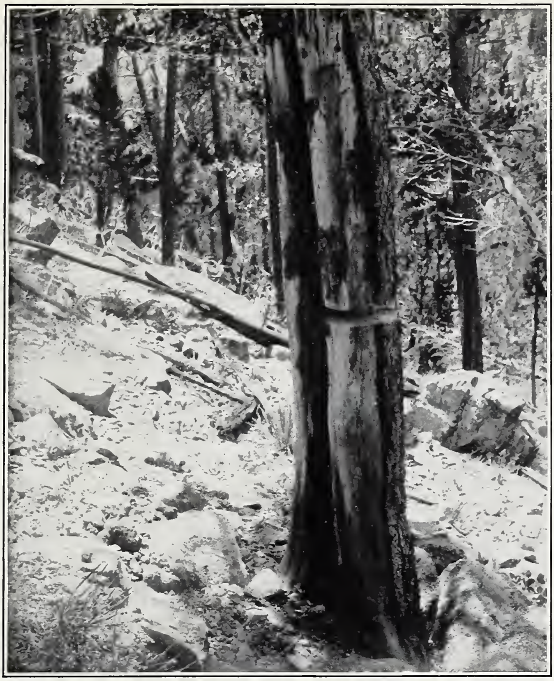

FIG. 1.—DOUBLE SCAR ON LIVING LODGEPOLE.

FIG. 2.—SECTION OF THE HEAL EDGE OF SCAR, SHOWING THE FOUR ANNUAL RINGS.

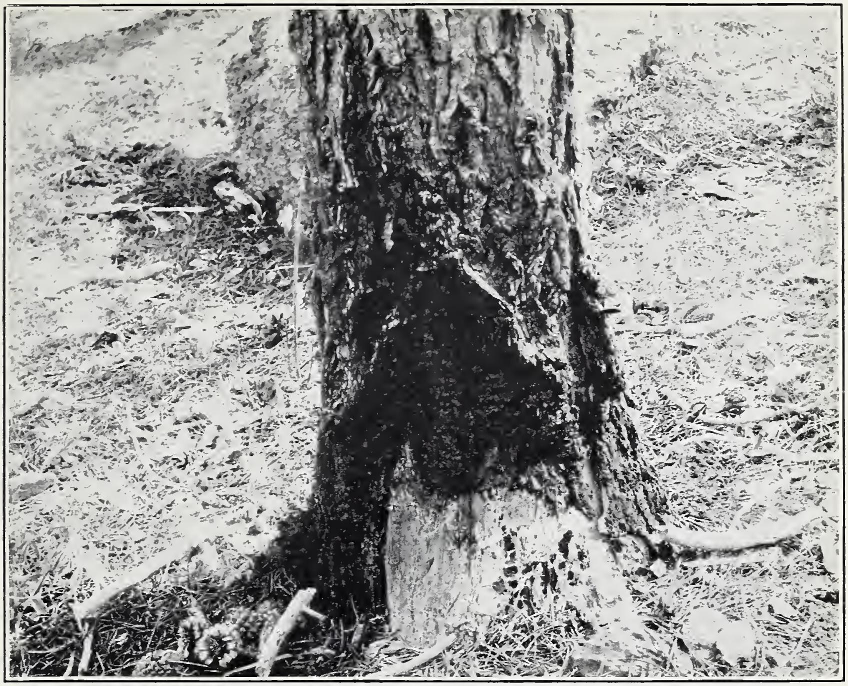

FIG. 1.—BASE BURN ON DOUGLAS FIR, FIRE OF 1905.

FIG. 2.—SECTION OF SCAR, SHOWING GROWTH AFTER TWO FIRES.

It is clear that fires, regardless of the place and manner in which they started, would have developed and spread most rapidly in the lodgepole-Douglas fir zone. Undoubtedly many fires started in the upper grass land, but practically all of these must have spent their force before passing through the open pine woodland, upon which they could have little effect. It is highly improbable also that fires could have developed or spread in the pine woodland itself. Fires could have started rarely, if at all, in the Engelmann spruce-alpine fir zone except when caused by lightning, because of the abundant moisture there. The position of the lodgepole-Douglas fir type, as the forest most touched by man, together with the dense character of its growth, marked it as the natural area for the work of fires.

The probable dates of the various burns studied are, in order of their occurrence, 1707, 1722, 1753, 1781, 1842, 1864, 1872, 1878, 1891, 1896, 1901, 1903, and 1905. With the exception of the last two, no authentic record of these dates exists. The dates of 1864, 1878, and 1901 are fairly well checked by local tradition, while of the others no evidence can now be obtained apart from that afforded by the study of the burns themselves. The last four burns are local, the one in 1896 affecting a very small area. The earlier burns are all more general, extending for several miles along the mountains which inclose the park. Those of 1864, 1872, and 1878 in many places are still clearly marked, and can be studied and mapped with some accuracy. The earlier ones are more obscure; the effect upon growth is less evident; fallen trees have completely disappeared through decay, and fire scars are found with difficulty. In consequence, while the occurrence of fires at these dates can be established, little can now be determined of their extent and effect.

METHODS OF RECONSTRUCTION.

The basic method of reconstructing a burn has been to determine the ages of the oldest plants which have come in since the fire, applied both to the trees and to the shrubs and perennial herbs of each type. It takes account of dead trees and shrubs, standing and fallen, in addition to the living ones. The method of fire scars is of equal importance, though often less available. Where the same area has been burned over two or more times this method is of unique value, for it is not unusual to find double and even triple scars. The nature, position, and extent of fire scars are of equal importance. Any evidence left by a fire upon a woody plant is regarded as a scar. Hence it is possible to distinguish top scars, trunk scars, and base scars with respect to position, and bark scars and wood scars with respect to depth. Heal scars and hidden scars occur on living trees, while white scars and cinder scars are found on dead or dying trees. In addition to ages and scars, the observation of soil layers is often of great help. The presence or absence of a cinder layer or of cinder pockets or of an organic layer or cover often goes far to check or confirm the evidence drawn from ages or scars. (See Plates II and III.)

The evidence of age drawn from annual rings is usually so clear and decisive as to be beyond question. Occasionally with seedlings, and often in the case of suppressed trees, it is impossible to make an absolute count of rings, even by means of microscopical sections. In practically all such cases an examination of other individuals is conclusive.

A distinction between fire scars and scars due to other causes is sometimes made with the greatest difficulty, and in rare cases is altogether impossible. In most cases, however, it is possible to recognize a fire scar with certainty. In actual practice the method was to require evidence of charring wherever the age of the scar did not check with that of neighboring scars. Chance scarring by lightning or by a camp fire, often in unexpected places, is of sufficient frequence to explain the departure of any charred scar from the normal. The position of a scar often serves to determine whether it belongs to a particular fire or is a mere chance scar. Heal scars abound at the edges of a burn, and consequently those caused by the same fire occur on the same side, namely, that from which the fire came. Occasional exceptions arise where a ground fire has unexpectedly worked to the surface, but these are nearly always determined by a careful scrutiny. The nature of fires and their severity is indicated, as a rule, by the depth of scars, and the predominance of bark scars or wood scars is used to determine the relative order of two or more successive fires. Scars from successive fires are often united in double or triple scars on either dead or living trees, and these give the best of all evidence upon the succession of fires and the burn forests which follow them. In using the depth or nature of scars as a guide the fact was considered that forests regularly contain dead standing trees, some of which may have lost their bark. It is evident that the same fire would cause at least three different kinds of scars in such stands; that is, heal scars, usually basal, on the surviving trees, bark scars on the living trees killed by the fire, and wood scars on the dead trees. The wood scars would, moreover, be cinder scars wherever the bark had fallen off before the fire had occurred. Finally, the data obtained from fire scars were checked by a count of the annual rings formed since the scar was made. The most careful use of the evidence from fire scars and from annual rings can not eliminate the possibility of an error of one year in determining the date of a fire. This is because the time of the growing season at which a fire occurs determines whether growth or germination may begin that year. With scars and root suckers on trees which remain alive, it is probable that growth begins the year of the fire, unless it occurred in the fall or early winter. On the other hand, it is equally probable that seeds remain dormant until the following year, unless the fire occurs in spring or early summer. The majority of fires occur after midsummer. If the growing season is not over, scars and root suckers will show one more ring than the pines and perennial herbs which appear the next year. If it is after growth ceases, scars, root sprouts, pine seedlings, and perennials will agree in the number of rings. In most of the burns studied scars formed the first ring the year of the fire, while the pine seed did not germinate until the next spring. In the burn of 1905 the aspen root sprouts followed the fire immediately, but in the burns of 1901 and 1878 aspens and pines appeared together the year after the fire. Therefore the following simple rule was used to determine the year of a fire: Subtract the number of rings of a scar, or the number of rings plus one of a seedling or tree, from the year in which the count is made. This rule assumes that the trunk is cut sufficiently low to show the first year's growth. With lodgepole it was necessary to cut the trunk at the surface of the ground, or on slopes below the surface.

BURNS OF 1905 AND 1903.

Opportunity did not permit a thorough study of either of these burns, in fact a mere glimpse was caught of the earlier one. Both fires occurred on the same ridge in the lodgepole forest, and the results obtained for the one held in general for the other. The fire of 1905, said to have started from a sawmill, occurred in July, sweeping up and down Millers Fork for a distance of several miles. The greatest damage was done in the lodgepole type, but the fire also ran down into the mixed forest of Douglas fir and yellow pine, and up into the Engelmann spruce. The burn was thorough, both on the ground and in the tops, though many groups of living trees were left. These stood along the stream, and especially on the rocky slopes and cliffs covered with an open stand of Engelmann spruce. In the lodgepole areas, the only trees which escaped were those in wet situations or in belts and tongues along the edge of the fire.

The ground cover and litter were completely burned, exposing the gravel soil as a seedbed. All the trees had been killed, though they stand thickly as in the living forest, and only in the more open places have any fallen. The bark was blackened but rarely burned through, and still remains intact on most of the trees. In the marginal zone of aspens, the general effect has been the same, except that the bark has begun to strip off, leaving the trees white and bare. The cone production of the burned lodgepoles was excellent, especially with the younger generation, which apparently sprang up after the fire of 1864. The great majority of cones on these were open.

The large trees in the burn were found to have 184 rings. Since they were killed in 1905, the oldest individuals must belong to a forest established about one hundred and eighty-seven years ago; that is, about 1720. Fire scars on these trees show 41 to 42 rings, and indicate a second fire in or near 1864. This is checked by living lodgepoles at the edge, which were found to be 42 years old, and by dead pines and aspens, which showed uniformly 38 rings. The discrepancy of one or two years is probably due to the small number of pines and aspens examined. The date of the last fire is fully attested by fire scars, and by the new pine, aspen, shrubs, and perennial herbs.

In the third year after the fire the ground cover was still open. In many places the gravel was entirely bare; in others it was completely covered by small mats of bearberry (*Arctostaphylos uva-ursi*) and of sedge (*Carex rossii*). Fireweed (*Chamænerium angustifolium*), raspberry (*Rubus strigosus*), *Drymocallis fissa*, *Senecio rosulatus*, goldenrod (*Solidago oreophila*), and milfoil (*Achillea lanulosa*), were also present. The ground was covered with a fairly continuous mossy layer, typically *Bryum argenteum* and *Funaria flava*, which constituted an excellent seed bed. The more open rocky slopes and ridges showed a very sparse cover of *Pentstemon humilis*, *Artemisia frigida*, *A. ludoviciana*, and *Ribes strigosus*.

In the area studied, lodgepole and aspen alone were sufficiently abundant to effect reproduction. The two trees were seldom mixed, the aspen occurring usually in belts and pockets. In consequence, the seedlings of each were found in separate areas, and had not yet come into competition with each other. Lodgepole reproduction was extremely variable, ranging from none on the steep rocky slopes, due as much to the roll of the cones as to the unfavorable conditions, to fair or good on level and moist open areas, and much poorer again in half-boggy places. It was never dense, but over much of the area was sufficient to insure a good stand. In the level areas reproduction was best where the seed trees were younger and crowded, and poorer near the larger trees. In the bare spots the seeding varied from fair to sparse, but the mats of bearberry were uniformly without seedlings, and in the cover everywhere the number was small. The best reproduction was along logs and especially among rocks down the small gullies, where the wash had carried the cones and seeds. (See Plate IV, fig. 2.)

Seedlings varied in height from 3 centimeters to 22 centimeters (1.2 to 8.7 inches), with the majority falling between 12 and 16 centimeters (4.7 to 6.3 inches), and in diameter from 1 millimeter to 4 millimeters (0.04 to 0.16 inch). Most of the smallest seedlings were on the rocky slopes and ridges, but some of the largest grew here also. The former, however, were found uniformly in the bearberry mats, the latter in open spaces, usually at the edge of a rock. The age of the seedlings was determined by microscopical study of 65 individuals, and in every case was found to be 3 years. This seemed to indicate conclusively that effective seeding took place only the first year after the fire.

In the burned aspen belts no pine seedlings were found. This is partly due to the absence of seed except at the edge, but chiefly to the competition of the young aspens. The latter arose as root suckers from the parent trees, nearly all of which remained alive below ground for some time after the fire had passed. The young shoots consequently grew very rapidly and were from 80 to 90 centimeters (31.5 to 35.4 inches) high and from 10 to 12 millimeters (0.39 to 0.47 inch) in diameter. They uniformly showed four rings, thus proving that they had developed from the burned parents shortly after the fire in 1905. In these areas the young aspens had possession of the ground when the lodgepole seeds began to germinate in 1906. Their roots were not only drying out the soil, but their foliage made a fairly uniform shade unfavorable to the pine. The latter could hardly be said to enter into competition with the aspens for water and light, since the aspens already had decisive control of both. Under such conditions it is clear that pines can not establish themselves in aspen areas, and that the latter will tend to maintain themselves through a series of fires whenever moisture makes it possible for root sprouting to result in a dense thicket-like stand. Certain aspen forests in Mills Park seem to afford proof of this. These have persisted in the same spot for a number of generations, though they are completely hemmed in and in some places actually invaded by pines.

THE BURN OF 1901.

The fire which caused this burn started at the southeast base of Moraine Ridge, sweeping northwestward around the base of the mountain, and upward to timber line. It burned upward in tongues, leaving alternating belts of half-burned and completely burned trees, often surrounding masses of unburned forest. No other burn studied shows such an extremely diverse character. While this is due in some degree to the topography and to the effect of slight barriers upon a slow fire, it is chiefly explained by the fact that the fire of 1901 occurred on the northwest portion of the burn of 1878. The completely burned belts of the last fire correspond to partially burned tongues at the edge of the fire of 1878 and the half-burned belts to the unburned portions between. This conclusion is supported by 22-year and 23-year heal scars on trees killed by the last fire and by cinder scars on dead standing and fallen trees. The result has been contiguous areas of complete burn, half burn, and unburned forest in two or more series. Since this is touched on nearly all sides by the burn of 1878 and includes the small area burned in 1891, it offers a unique opportunity for the study of burn reproduction.

The value of the burn for purposes of investigation is enhanced by the different forest types included in it. At the base of the ridge it includes part of the mixed lodgepole-aspen forest which sprang up after the fire of 1878. The major part of the fire was in practically pure lodgepole forest. On the rocky ridges, however, it was in pure stands of limber pine, in a mixture of this and lodgepole, or, toward timber line, in limber pine and Engelmann spruce. The higher slopes as far as timber line show the effects of fire in pure Engelmann spruce or in mixtures of this with alpine fir. (See Frontispiece.)

The mature forest on Moraine Ridge consists of trees of two different generations, dating apparently from fires in 1707 and 1753. The unburned areas show the characteristic features of mature lodgepole forest. The trees stand close together, making an almost continuous shade. The crowns are small and touch each other. For their size, the number of cones they bear is large. Undergrowth is practically absent throughout, particularly in the denser areas where Pterospora, mosses, and lichens alone were found. The ground is carpeted with a layer of pine needles, varying from a half inch to several inches in thickness. In all such areas reproduction is impossible. During the investigation, except in open places, not a single lodgepole seedling was found in the mature forests. All the conditions seem to conspire to the same end. Rodents keep the seed supply down to a minimum, the needle cover makes a poor seed bed, and the light is not sufficient for the seedlings that start. The effect of water content of the soil seems less decisive, since it could hardly be exerted in competition until seedlings were 2 or 3 years old. It is significant that no such plants are found.

Conditions in the half burn are intermediate between those of the mature forest and those of the open. The proportion of living trees varies from one-third to two-thirds. Fire has run through the tops in such a way as to leave living and dead trees in an almost uniform mixture. The ground fire has swept away the needle layer and exposed the soil. This preparation of a seed bed, together with the opening of the leaf canopy, has permitted the development of a characteristic cover of pioneers, foremost of which are fireweed (*Chamænerium angustifolium*) and blueberry (*Vaccinium oreophilum*). These are really the species of the first stage of a burn succession, but where the trees are still alive they are at the same time the herbaceous ground cover. Even when in mixture, one is usually predominant. Often, however, one alone occupies large areas. When such is the case, Chamænerium usually occupies the drier rocky or gravelly areas and Vaccinium the moister humus soils. The fireweed is rather uniformly distributed, but rarely dense, while the blueberry usually forms dense mats and carpets. The latter evidently enters into keener competition with the seedling pines, though it affects the rate of growth rather than the number. (See Plate V, fig. 1.)

The fire grass (*Agrostis hiemalis*) and a mat sedge (*Carex rossii*) are among the most important associates. The fire grass is especially plentiful in the complete burns, where it is usually dominant. Raspberry and sedge are found chiefly in the half burns, though they occur sparsely throughout. *Phacelia lyallii*, *Achillea lanulosa*, *Arnica cordifolia*, and *Solidago parryi* are all abundant in places, and are sometimes characteristic. A few species, *Trisetum subspicatum*, *Bromus ciliatus*, *Thermopsis divaricarpa*, *Anaphalis margaritacea*, *Senecio macdougalii*, *Sedum stenopetalum*, etc., occur here and there, but are unimportant. Beneath the open herbaceous cover are Bryum and Funaria, often with Cladonia and Peltigera, of some value perhaps in keeping the seed bed moist.

Varying in number with the amount of shade, the number of dead cone-bearing trees, the slope, and the cover, seedlings occur throughout the half burns with the exception of some nearly bare areas, probably due to snow remaining so late in the year that seed does not germinate. Owing to the roll of cones and the washing of cones and seeds, few seedlings are found on the slopes. The maximum seeding in the half burns occurs just below steep slopes, especially those partly covered with snow or with large bowlders, or with both. In such situations, as many as 140 pine seedlings were found in a 10-meter quadrat (a square, 32.8 feet on a side, equals one-fortieth of an acre, very nearly). A 2-meter (6.6-foot) transect, 55 meters (180.4 feet) long, contained 186 seedlings, an average of one and two-thirds to each square meter (1.2 square yards). The greatest density was 9 seedlings to the meter ($7\frac{1}{2}$ seedlings per square yard).

The ages of the pine seedlings range from 4 to 7 years, those of 6 years being in the majority. The young aspens are uniformly 7 years old, indicating that they started from root suckers the year after the fire. This indicates that the fire occurred after the middle of summer, too late for the aspens to begin their growth the same year. The height of the seedlings varies from 1 centimeter to 50 centimeters (0.4 to 19.7 inches), the largest ones occurring at the edge of large bowlders, or near the margin of the complete burn where the light was stronger. The seedlings in the half burns are scarcely half as high as those in the complete burns, and are correspondingly smaller in diameter. Owing to their greater protection, however, they have suffered but little from the winterkilling which had been so marked with the pine seedlings in the open.

The complete burns are of two sorts, those in which the dead trees are still standing, and those in which they are down. The difference in reproduction comes from the reduced light intensity in the areas with standing trees, and is chiefly one of growth rather than of density. The position of the trees seems to have little or no effect upon the amount of seeding.

Although the burns with dead but standing trees give the effect of being shady, measurements indicate that the light is much stronger there than in the half burns. The number of cones is approximately the same in each, though in the standing burns more of the old closed cones were opened by the fire. The ground cover is usually more dense and better developed, and the competition between cover and seedlings, especially where the cover is Vaccinium, is often striking. Chamænerium and Vaccinium are the chief species of the cover. *Rubus strigosus*, *Arnica cordifolia*, *Carex rossii*, *Agrostis hiemalis*, and *Rosa engelmannii* are frequent, but rarely dominant. The more open nature of the burn is shown by the entrance of *Artemisia frigida*, which is somewhat characteristic in the bare burns. The soil, a moist sand topped by an inch of needle mold and charcoal, is rich in carbon, and is covered by a fairly uniform layer of moss.

The maximum reproduction per unit area in the " standing burns " exceeds that found in any other place. One 10-meter quadrat gave a total of 523 seedling pines, an average of 5 to the square meter (1.2 square yards) and a maximum of 34. This last is equivalent to a density of 138,000 per acre. A second quadrat, charted in a dense Vaccinium cover, gave 297 seedlings. The seedlings are sparse on the slopes, except gentle ones, but are denser in all level areas and in hollows. In the Vaccinium areas, they are rather uniformly distributed, but elsewhere are extremely gregarious, the dense groups occurring where the cover was lacking. The age varied from 4 to 7 years, with the majority 6 years old. Rare individuals of aspen varied from 4 to 7 years, though usually of the latter age. Vaccinium stems usually showed six rings, indicating that the cover and the pines had both started about the same time. In the fireweed, five or six rings were found, indicating clearly that it had also entered soon after the fire. The seedlings ranged from 4 to 70 centimeters (1.6 to 27.6 inches) in height and from 2 to 13 millimeters (0.08 to 0.51 inch) in diameter. They showed the effect of winterkilling but slightly, though in the denser groups the consequence of competition was marked. Except where competition was keen, the growth of internodes in 1907 averaged 12 centimeters (4.7 inches), in 1908, 15 centimeters (5.9 inches). (See Plate V, fig. 2.)

The standing trees, most of which are on the rocky slopes, are far apart, with the result that the ground cover receives more light, but has a smaller water supply. In general, the bare burns, where all the trees have fallen, show similar conditions, except that in them the number of cones on the ground is usually greater, and the reproduction better. Moreover, the ground cover is much more uniform

FIG. 1.—REPRODUCTION IN A BARE BURN.

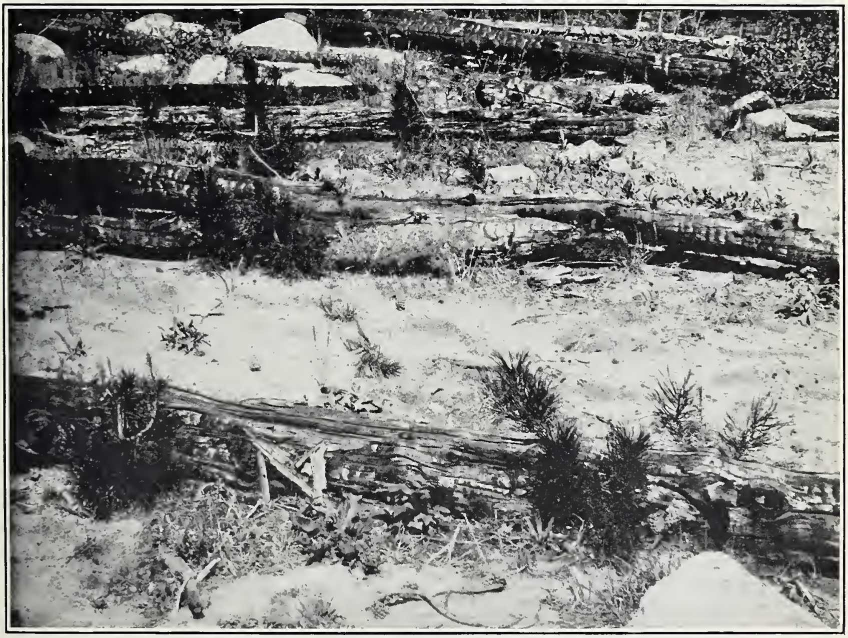

FIG. 2.—REPRODUCTION IN A GULLY, SHOWING HOW LOGS HELP TO ESTABLISH SEEDLINGS.

FIG. 1.—REPRODUCTION IN A HALF-BURN.

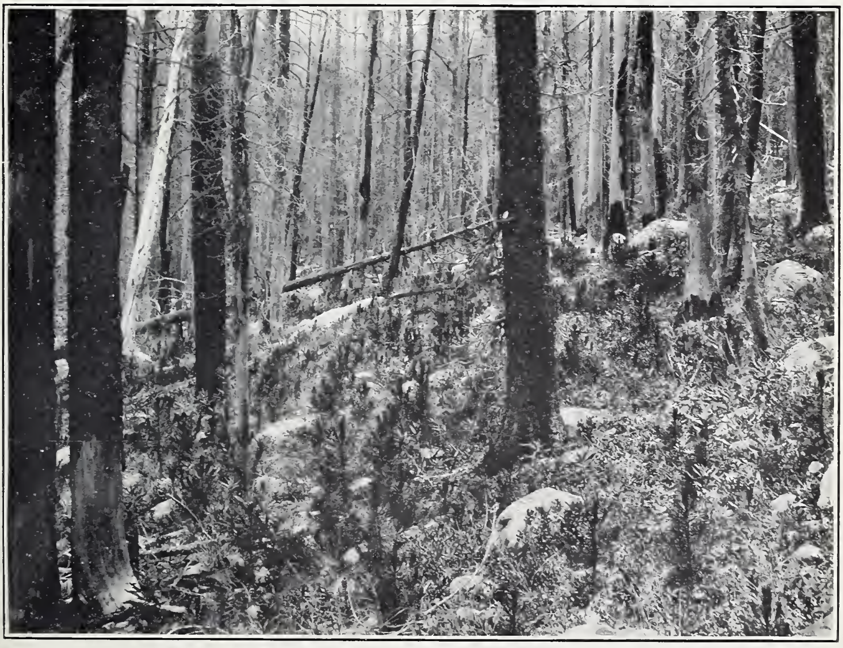

FIG. 2.—REPRODUCTION IN A STANDING BURN.

and dense, and enters more into competition with the pine seedlings. In it *Agrostis hiemalis* has an unusually thorough control. With these important exceptions, the account of the bare burns applies to these related areas in which many trees are standing.

The most typical bare burns are tangles of rocks and logs, which cover a half or more of the surface. The soil is almost pure gravel, still showing much charcoal from the last fire. There are no standing trunks to decrease the light, and conditions for germination and growth are at their best. The large number of rocks and logs prevent roll and wash and readily explain the more uniform distribution of the seedlings. The latter are found almost without exception in the shelter of a rock or pebble. This position has the advantage of increasing the water supply of the seedling. The cover is of the open-gravel slide type, in which individuals stand separately or in loose groups. This doubtless does more good in increasing water and humus content than injury by competing with the pine seedlings. The species of the cover form no definite societies, but are intermingled throughout. Rare exceptions occur only near half burns or standing burns. *Phacelia lyallii*, *Rubus strigosus*, *Carex rossii*, and *Chamænerium angustifolium* are the most important. Vaccinium and Agrostis are usually less abundant, especially in the most rocky places. Vaccinium and Chamænerium increase conspicuously near the half burns, in which they are typical, and Agrostis similarly toward the areas in which it is controlling. *Achillea lanulosa*, *Arnica cordifolia*, *Thermopsis divaricarpa*, *Carex siccata*, *Phacelia heterophylla*, *Fragaria glauca*, *Senecio macdougalii*, and *Anaphalis margaritacea* are all more or less frequent. Woody species, Vaccinium, Rubus, Rosa, and Sambucus play no distinct part. They are merged with the herbaceous forms, which are followed directly by the new growth of lodgepole without the intervention of a distinct thicket or chaparral.

In quantity of reproduction the bare burns fall short of the standing burns in maximum seeding. A 10-meter quadrat near the edge of a bare area yielded 270 seedlings, practically an average of 3 to the square meter (1.2 square yards). A 2-meter (6.6 feet) transect through the heart of the same area gave a total of 235, or about 1 to every meter. The maximum found in a single square meter (1.2 square yards) was 8. The distribution of seedlings is so much more uniform that the bare burns equal, and probably exceed, all other areas of like extent in the total number of young pines. The quality of the reproduction is, however, much more significant. The maximum height of seedlings is about 100 centimeters (39.4 inches) and the diameter 2.5 centimeters (1 inch). The average height and diameter exceed those in the best areas of the standing burn by one-fourth to one-third. The seedlings are especially stocky and well branched in comparison with the more slender ones of the shaded areas. (See Plate IV, fig. 1.)

The great exposure of seedlings on the bare burns has resulted in extensive winterkilling, occasionally of the whole plant, but, as a rule, only of one or more branches or nodes. Careful scrutiny showed that it was the growth of 1907 alone that was seriously affected. A few of the smaller and more exposed seedlings were dead when examined. Practically a half of the seedlings in one of the quadrats showed the growth of 1907 to be browned in the internode or in one or more of the branches. In certain small areas with peculiar exposure the number was greater. On slopes protected from the northwest the percentage of injured seedlings decreased in direct relation to the protection until, in the half-burn belts, browned individuals were scarcely to be found.

THE BURN OF 1896.

This fire seems to have played no part in the lodgepole reproduction of Mills Park, and the evidence indicates that only a very few trees were affected. While studying the burns of 1878 and 1864, basal 12-year-old scars, indicating a fire in 1896, were found on a few trees. Further than being of value in affording a warrant for the exclusion of contradictory evidence in older burns where the presence of a small chance burn could no longer be detected, this fire was of scarcely any importance.

THE BURN OF 1891.

This fire occurred at the northeast base of Moraine Slope and extended over a few acres only. At the east and north it began in the growth which marked the burn of 1878, and at the upper edge it was in turn invaded by the fire of 1901. Its importance is necessarily small because of its small area, but as a link between two general burns its ecological importance is great.

The majority of the trees studied were 16 years old, but two showed 18 rings. Occasional individuals of 14 and 15 years were found. The general evidence points to a fire in 1891, followed by seeding the next year, with occasional seeds germinating in 1892 and 1893. It is impossible to explain satisfactorily the presence of the 18-year-old trees, and the exact date of the fire must remain in doubt for the present.

The fire probably occurred partly in the mixed aspen and lodgepole characteristic at this point of the burn of 1878 and partly in the mature forest on the ridge. In the older forest the gravel soil must have been covered with a needle layer, and in the growth which started in 1879 with an herbaceous layer somewhat similar to that in the burn of 1901. This cover was burned off, leaving a gravel seed bed exposed to the full sunlight. The number of cones on the young trees of 14 years must have been small, and the seeding undoubtedly came from the mature trees higher up the slope. The saplings apparently cover only that part of the burn which could be seeded from the mature trees, a conclusion borne out by the fact that about one-half of the area burned bears only an occasional seedling.

The cover to-day is open and consists of a few species. The chief of these are *Agrostis hiemalis*, *Trisetum subspicatum*, *Arctostaphylos uva-ursi*, *Arnica cordifolia*, *Lupinus decumbens*, *Achillea lanulosa*, and *Senecio anacletus*, with Chamænerium, Drymocallis, Rosa, Sambucus, Phacelia, etc., less frequent.

The young pines occupy a long, narrow strip, due partly to the sweep of the fire and the flight and roll of seeds and cones. As already described, only that part of the burn toward the ridge was well seeded after the fire. The remainder doubtless developed a few seedlings, but these were destroyed in the fire of 1901, the edge of which encircled the main group of young pines, killing them on the upper side, where it swept over the ridge, but on the lower side merely scarring the seedlings and charring the fallen logs. The pines that remain are very thrifty. They are closely crowded, however, and the resulting competition has produced a marked difference in growth. The trees are essentially even aged, varying from 14 to 16, rarely 18, years. In size they vary from 0.5 meter to 3.6 meters (1.6 to 11.8 feet) in height, and from 1.6 centimeters to 10 centimeters (0.6 to 3.9 inches) in diameter.

Except on the 18-year-old trees, cone production is just beginning. The small number of seeds does not promise reproduction. In spite of the fact that the open gravel between the groups furnishes an opportunity for germination, not a single seedling was found. Moreover, it is improbable that even a large increase in the number of cones will bring about reproduction under present conditions.

THE BURN OF 1878.

This burn covered the major portion of Allan Park, from which it spread northward into Mills Park and northwestward up the slopes of Mount Meeker. Its advance through the valley seems to have been rather steady and uniform, as shown by the fact that its extreme northern limits on the west and east walls of the park are opposite each other. The fire swept across the whole valley, burning everything except the open yellow-pine woodland on the ridges and park-like areas in the middle. Its force diminished in the neighborhood of Longs Peak Inn, and in consequence it became erratic, jumping from one area to another. This was especially the case on the lower slopes of Twin Mountains, where three burned areas alternate with belts of the original forest.

The original forests in which the 1878 fire occurred are still clearly indicated by the fragments left. The central portion of Mills Park was occupied by a very open woodland of yellow pine 300 to 400 years old. Mingled with this, especially at the edges, were younger aspen woodlands. On the bases of the slopes the yellow pine formed a closer forest before yielding to lodgepole and Douglas fir. In some places lodgepole formed pure stands, but on the western slopes especially it was associated with Douglas fir and some Engelmann spruce. On the west wall of the park lodgepole and limber pine alternated in nearly pure stands. Above this they gave way to Engelmann spruce and alpine fir in nearly equal mixture. To the west the fire came to an abrupt stop in these two types, but on the east it ran out more irregularly, finally stopping in the Douglas fir, lodgepole, and yellow pine. Although the majority of trees examined were 28 years old, a number showed 29 rings, which would make the date of the fire 1878. This is supported by the evidence obtained from heal scars on mature trees afterwards killed by the fire of 1901. The vegetation which now covers the burned area consists of four different types, which repeatedly alternate. These are (1) pure stands of aspen, (2) mixtures of aspen and lodgepole, (3) pure lodgepole, and (4) mixed lodgepole and yellow pine. Their position and structure have been determined by the place of the parent trees in the original forest. Under present conditions all four areas will maintain themselves for many years to come. In the course of several decades the aspen-lodgepole mixture will become lodgepole forest, and in most situations a similar fate will overtake the pure aspen stands, though much more slowly.

Pure aspen stands, though not extensive, occur frequently. They usually occupy the central, more level portion of the park, chiefly where the yellow-pine woodland has disappeared. The growth is thicket-like on the drier ridges, but elsewhere the trees are somewhat clustered. The individuals range from 3 to 5 meters (10 to 16 feet) in height and from 4 to 8 centimeters (1.6 to 3.1 inches) in diameter. The leaf canopy is open, permitting the sunlight to pass through, and resulting in the development of a continuous herbaceous ground cover. The latter consists typically of Thermopsis, with Chamænerium and Castilleia as important associates. Of less importance but regularly present are *Lupinus decumbens*, *Geranium richardsonii*, *Galium boreale*, *Aragallus lamberti*, *Pedicularis procera*, *Campanula petiolata*, *Arnica cordifolia*, *Rosa engelmannii*, *Calochortus gunnisonii*, *Fragaria glauca*, and *Pseudocymopterus tenuifolius*. The gravel soil contains much humus and is covered with a thin layer of leaf mold.

The mixed aspen-lodgepole forests exhibit a wide range of conditions and structure. They alternate with the pure aspen stands in the middle of the park, and extend as a more or less continuous transition zone around the base of the lodgepole forests on the slopes. In the more typical areas, the trees are on somewhat equal terms. The very nature of their reproduction from the parent trees causes them to appear in a more or less distinct group arrangement, which is of considerable importance in future reproduction. This grouping interrupts the leaf canopy, gives a more open nature to the forest, and permits the entrance of more sunlight. It has a similar effect in breaking up the herbaceous layer and leaving small areas with little or no cover. The pines and aspens are at present nearly equal in height, though the individual variation is great. The majority range from 4 to 6 meters (13 to 20 feet) in height. When they are not crowded in groups, the lodgepoles have a much greater diameter, usually from 10 to 15 centimeters (4 to 6 inches), while the aspens range from 5 to 8 centimeters (2 to 3 inches).

The herbaceous undergrowth is much like that in the aspen forest. It is practically identical where the aspens predominate, but gradually changes whenever the pines increase. Thermopsis, Chamænerium, *Solidago oreophila*, Lupinus, Castilleia, and *Arnica cordifolia* are the most characteristic. Mats of Arctostaphylos are frequent and of special importance among the pines. *Fragaria glauca*, Achillea, Rosa, Galium, etc., occur regularly, but with the exception of the first are rarely controlling. Where the pines are more numerous, the layer becomes very sparse and finally, in the copse-like groups, disappears entirely, the ground being covered by a dense layer of brown needles. Many of the characteristic species of the aspen persist, and are joined by others from the gravel slopes and rock ridges. The density of the individuals diminishes correspondingly until but one or two are regularly found in a square meter (1.2 square yards). In addition to Thermopsis, Castilleia, Lupinus, Galium, Chamænerium, Solidago, etc., found among the aspens, *Gaillardia pinnatifida*, *Drymocallis fissa*, *Draba streptocarpa*, *Potentilla coloradensis*, *Pentstemon humilis*, *Erigeron multifidus*, *Sedum stenopetalum*, *Artemisia ludoviciana*, *A. gnaphalodes*, and *A. frigida* have come in from the drier areas.

The cone production of the 28-year lodgepoles is good, especially where they occur singly or in small groups. The number of open cones upon each tree usually exceeds the number of closed ones. The few cones found upon the ground are practically all open. The others cling so tightly to the branches that they are rarely dislodged, and distribution can be expected only by rodents cutting off cones or branches, or by the wind. The effect of the latter is clearly shown by occasional clumps which are fully exposed to the wind. The space beneath the pines contains no seedlings, but the latter first appear about 10 meters (33 feet) to the southeast of the group, become more numerous, and finally straggle away, disappearing about 50 meters (164 feet) from the parent trees.

Because of the heavy toll upon the fallen seed by chipmunks, squirrels, and birds, the open spaces among the aspens and between the aspens and the lodgepole clumps, which afford fair conditions for germination and growth, are wholly or largely without seedlings. Circumstances temporarily more favorable to seeding seem to have occurred the year preceding, and also five to seven years earlier, since practically all of the scattered seedlings belong to one period or the other. The five to seven year pines are rare, and serve to emphasize the infrequency of germination. The tiny one-year seedlings are equally rare, except where the pines become much more numerous and the number of seeds correspondingly large. A 10-meter quadrat in such an area gave a total of 25 seedlings, all 1 year old.

The pure lodgepole stand covers the park-like valley toward the St. Vrain. Always dense, it becomes thicket-like and almost impenetrable on the drier ridges. Almost all the dead trunks of the parent pines have fallen and now cover a large part of the ground. Their cones have disappeared, and they play little part except in decreasing the light received by the ground cover.

The gravel soil is carpeted with needles an inch or two deep, and with many plants of Peltigera and Cladonia. The herbaceous layer is thin and often interrupted. It nowhere makes a compact cover, but even in the more open places the plants are numerous enough to compete with the seedlings for moisture. Drymocallis, Campanula, Thermopsis, Galium, Erigeron, and Solidago are the most important, with *Koeleria cristata*, *Geranium cæspitosum*, *Antennaria parvifolia*, *Gentiana parryi*, *Rosa engelmannii*, *Lupinus decumbens*, *Sedum stenopetalum*, *Achillea lanulosa*, and *Arabis oxyphylla* scattered here and there.

The lodgepoles vary from 5 to 10 meters (16 to 33 feet) in height, the average being from 7 to 8 meters (23 to 26 feet). In diameter they range from 4 to 15 centimeters (1.6 to 5.9 inches), the majority falling near 10 centimeters (3.9 inches). Owing to the dense grouping and rapid growth of the trees, cone production is small. Except in occasional spots where the stand is more open, reproduction is almost entirely absent. Even the seedlings which have started are already suppressed, and can take no effective part in the development of the forest.

The lodgepole yellow-pine mixture occurs on the west slope of South Twin Mountain, where the soil is bare and rocky. A part of the slope bears a uniform but somewhat open stand of lodgepole, while over much of it has developed a low, thicket-like cover, in which both pines are widely scattered. On the middle slope they are about equal in number. Along the base yellow pines become the more numerous toward the parent area, while northward along the original forest, Douglas fir and an occasional limber pine appear. The typical species of the open cover is *Edwinia americana*, with *Juniperus sibirica* and *Ribes pumilum* scattered in it. *Koeleria cristata* and *Calamagrostis purpurascens* are the chief grasses and are usually associated in very open communities. The chief community on the open slope is that of *Thermopsis divaricarpa*, and with it occur much Chamænerium, Erigeron, and Chrysopsis. Arctostaphylos (the bearberry) forms characteristic and often extensive mats toward the edges of the open area. *Artemisia gnaphalodes* and *Drymocallis fissa* make small open communities, either alone or together. *Solidago oreophila*, *Arenaria fendleri*, *Sedum stenopetalum*, *Achillea millefolium*, *Artemisia frigida*, *A. ludoviciana*, and *Geranium cæspitosum* are common in the open drier places.

The slope is thickly covered with fallen logs, with here and there a standing tree. Cones have practically all disappeared. The cone production of the new lodgepoles in the denser stands at the edges is only fair, and is poor among the smaller trees of the same age on the open slope. Though the ground is fairly well covered, the gravel in many small patches is sufficiently exposed to permit seeding. The largest lodgepoles are 29 years old, and average 4.5 meters (14.8 feet) in height and 20 centimeters (7.9 inches) in diameter. The largest yellow pines of the same age are 2.5 meters (8.2 feet) high and 12 centimeters (4.7 inches) in diameter. Trees of both species which averaged 1 meter (3.3 feet) in height were found to be 21 and 22 years old, indicating a seeding period at this time. Young seedlings a few years old are rare. The maximum number found in a single quadrat was 4, while by far the larger number of quadrats contained no seedlings. The forest cover of the slope will for a long time be an open woodland of mixed lodgepole and yellow pine. It is improbable that its nature could be essentially changed without the agency of another fire, after the trees are mature enough to produce a large supply of cones.

THE BURN OF 1864.

It is all but certain that the fire which occurred in the year 1864 started along the base of the Continental Divide in Estes Park proper. Its northern limits have not been determined, but it moved eastward to the low range which terminates in Lillies Peak, and then swept southward through Wind River Canyon and Rock Dale. It entered Mills Park at the north end and passed almost completely around Estes Cone and along the base of Battle Mountain on the west and over the slopes of Twin Mountain on the east. On the west side, the fire burned uniformly, finally stopping in the rocky region just north of the Longs Peak trail. On the east side, it jumped as it turned North Twin Peak, leaving a broad belt of the mature forest, and then burned the entire western slope before it stopped at the north edge of South Twin Peak.

The fire of 1864 was the most extensive of the whole series of recent fires. In addition to the area actually covered, it is most interesting because of its range and altitude. The fire probably started in the lodgepole type, but in more than one place it burned upward through the belt of Engelmann spruce and alpine fir to timber line, and downward into the open woodland of yellow pine.

The conditions which brought about the reforestation of the burn have long ago disappeared. They can be conjectured, however, both from the development of the more recent burns and the location and structure of the new forest. In general, a pure lodgepole forest has established itself upon the remains of a mixed forest, wherever physical conditions have not been more favorable to another species. Except along the lower and the upper edge and on certain moist slopes, an almost pure lodgepole forest now covers the burn. At lower altitudes, on the drier western slopes, yellow pine and Douglas fir have reproduced more abundantly, and the new growth is essentially the same as that swept away by the fire. On the eastern slopes at the same elevation, lodgepole has been able to form pure, dense stands, in some cases among mature yellow pine and fir. Higher up, lodgepole has not been able to establish itself beyond 10,500 feet, and, as a forest, rarely above 10,000 feet. On the slope of North Twin Peak, where the drainage from the higher gravel slides accumulates, the high water content of the rich soil has made it possible for aspen to maintain itself in nearly pure pockets.

The reproduction which led to the forest growth on this burn must have been remarkable. Twelve hundred and fifty-six trees to the 10-meter quadrat, or more than 50,000 trees to the acre, was the maximum density, and the average number per square meter (1.2 square yards) was 11. Through the greater part of the forest, the density was less than one-tenth of the maximum. While the size of the individuals shows some variation with the water content of the soil, it depends, as shown in the table on page 46, much more upon competition.

A majority of the trees examined showed 42 or 43 annual rings. This checks with a large number of fire scars studied which gave uniformly 44 rings. Few trees either 40 or 41 years old were found, but trees of 38 and 39 years were fairly common. Apparently the seeding followed the rule, inasmuch as the maximum occurred during the first two years. The causes for rather uniform seeding two years later are too remote to be discovered now, but probably came from favorable seasons.

Cone production varies most strikingly with the density, and in considerable measure with the altitude. In the normal stand the largest number of cones found upon one tree was 1,475, the average falling near 500. Under the closest competition the maximum rarely exceeded 50 and the average was about 20. The great majority of the cones are open, though many of those of the last ten years still remain closed.

The ground cover is extremely sparse and of importance only where the stand becomes somewhat open or is mixed with aspen. Thermopsis is most common in the more open areas, while Lupinus is characteristic of the denser pine stands. Arctostaphylos forms small mats, particularly where the burn touches the original forest. Chamænerium, which must have been typical of the first undergrowth, almost disappeared as the light grew weaker, and is now scattered here and there. *Drymocallis fissa*, *Solidago oreophila*, *Draba streptocarpa*, *Achillea lanulosa*, *Senecio rosulatus*, *Pentstemon humilis*, *Rosa sayii*, and *Sedum stenopetalum*, all inhabitants of the open gravel slopes, occur sparingly.

Conditions for reproduction are scarcely, if at all, better than in a mature lodgepole forest, though the herbaceous cover presents little or no competition, and the cone supply is entirely adequate. Because of the density of the stand, and the consequent competition for moisture and light, not a single seedling less than 15 years old was found. Reproduction is completely at a standstill, and the forest is closed to all species except those capable of developing in deep shade.

In Wind River Canyon, at altitudes of from 7,500 to 7,800 feet, the burn shows three kinds of reproduction—lodgepole, aspen, and Douglas fir-yellow pine-lodgepole in juxtaposition. A close comparison of the different areas shows that while the number and distribution of the seedlings are direct results of cone production and position of the parent, both generations are controlled at bottom by the physical factors. In a word, the fundamental control is that of water, as expressed in the more complex factors of altitude, slope, and exposure. As a pure stand, aspen can occupy only the narrow valley along the brook, or the moist depressions and pockets on the west side. Lodgepole covers the west side with a dense forest, interrupted only by aspen in the moister areas, and by mixed Douglas fir and yellow pine on the dry rocky ridges. The east side, with west and southwest exposure, is much drier. Lodgepole covers only the head of the canyon, but yields to fir and yellow pine at a point much higher than on the west. In the valley it extends to lower elevations, together with both Engelmann spruce and alpine fir, here far below their proper zone. On the most exposed and driest slopes the new growth is almost wholly fir and yellow pine, with Douglas fir, as a rule, slightly the more abundant. Except at the head of the canyon, lodgepole plays an entirely subordinate part, and the new forest will essentially repeat the old; that is, it will be a mixed forest of Douglas fir and yellow pine, with lodgepole scattered through it and most abundant toward the edges.

Along the transition line between the lodgepole and the Engelmann spruce-alpine fir types, at an altitude of about 10,000 feet, lodgepole fails to hold its own, and is quite incapable of invading the burned portion of the spruce-fir type. In fact, the upper type is slowly invading the lower. The line between the two represents the extreme upper limit of lodgepole, but it is far above the lower limit of Engelmann spruce, alpine fir, and limber pine. All of these, but especially the spruce and fir, can reproduce in the shade of lodgepole, especially at these elevations, where they are less densely crowded. Lodgepole, on the other hand, is quite incapable of growing in the shade of spruce and fir. A third factor of the greatest importance is the action of gravity in determining the direction of movement of cones and seeds. The cones of the three species of the timber-line zone are readily carried downward, but it is all but impossible for those of the lodgepole to move upward.

The relative reproduction of the four species is well illustrated by a series of three 10-meter quadrats charted in the 44-year burn west of Estes Cone. The first, at an altitude of 10,500 feet, gave 3 lodgepole pines and 6 limber pines; the second, on a level area a little above, contained 4 lodgepoles, 2 limber pines, and 3 Engelmann spruces; the third, at 10,650 feet and just at the edge of a relict belt of the original forest, showed 45 Engelmann spruces, 23 firs, and 1 lodgepole. These results indicate also the slowness with which reproduction occurs at high altitudes, except, as in the third quadrat, where living trees escape the fire. The cones of the three species of the upper type were completely destroyed by fire, and those of the lodgepole were too few to bring about effective seeding.

Within the lodgepole stand on the west slope of North Twin Peak are three aspen areas. Evidence from fallen and moldering logs indicated that aspens had occupied these areas for at least two or three generations, and probably for many more. It is impossible to ascertain to-day just what determined that aspen and not pine should occupy the ground, but it is more than probable that the water content was the decisive factor. The areas are very shallow valleys or depressions in line with the surface and underground drainage of the extensive gravel and rock fields on the upper slopes of the mountains, and the soil is leaf mold, capable of retaining a large amount of water. In consequence, portions of the area are somewhat boggy. The advantage originally gained by aspen from the excessive moisture was maintained after each fire by its ability to at once send out root sprouts and take complete possession of the ground. Undoubtedly, pine cones and seeds were carried into these areas, but the young seedlings were unable to grow in the shade of the aspen sprouts. As the aspens grew taller the weaker ones were eliminated, and the shade of the leaf canopy became lighter. At the same time, however, the herbaceous species steadily increased, and this new layer increased both the unfavorable light conditions at the surface of the soil and the competition for water. Thus the conditions for pine reproduction have grown steadily worse, and the control exerted by the aspens has become absolute.

THE BURN OF 1842.

The north slope of North Twin Peak is covered above with the forest of the 44-year burn. On the lower half of the slope, especially along the road to Longs Peak Inn, this fire ran into the original forest of 154 years in two or three broad tongues, to-day shown by the alternation of belts of the 44-year and 154-year forests. Many of the trees in the larger belt of the 154-year growth were scarred at the base on the south and southeast side. The number of rings in every scar studied was 66, making the probable date of the fire 1842. This was not entirely confirmed by the number of rings found in trees in the limited area affected by the fire, where the oldest trees examined contained but from 62 to 63 rings. The number of trees, however, was too small to be conclusive.

The fire seems to have been a ground fire, which did little more than burn off the needle layer and scar the bases of many of the trees. On only one small area had any of the original trees been killed. In consequence, the fire brought about little increase in the number of seeds available for germination, and but a slight improvement in the amount of sunlight. This is borne out by the fact that Douglas fir has reproduced fairly well, while lodgepoles are infrequent, except toward the opening along the road. Fir has become dominant, in spite of the fact that it formed only about a tenth of the original forest. Its success arises from its ability to grow under moderate shade, in which lodgepole reproduction is impossible.

THE FIRES OF 1781, 1753, 1722, AND 1707.

Evidences of these four fires are found throughout the mature forest, and in the relict belts of it which have been left by later fires. While the four fires all played a part in the original forest, their effects have merged completely. The time that has elapsed since the most recent of them is more than sufficient to give a lodgepole forest its typically closed structure. Moreover, since it is practically impossible, on account of differences in habitat and competition, to distinguish the trees of the various burns without counting the number of rings, there is no way of differentiating the burns without counting the annual rings in hundreds of trees, which would be of little present value.

The fire of 1781 is determined with much certainty by the presence of scarred trees in the lower part of Chasm Canyon. It occurred in the more open lodgepole forest of the rocky canyon sides, and seems to have done little more than scar the trees, when they were about 55 years old, without essentially modifying the forest or initiating a new burn growth. The dates of the other fires can only be approximated. On the west slopes of Twin Mountains, the majority of the trees cut showed from 150 to 154 rings, usually either 153 or 154. A second group of ages ran from 178 to 185, most of them from 183 to 185. On the west side of the Park, along Estes Cone and Battle Mountain, all of the trees examined fell into one or the other of these groups. Along Moraine Ridge the mature trees belong almost wholly to the 185-year burn. In the lower valleys and southward toward the St. Vrain they range from 200 to 210 years. The oldest trees found in the most typical lodgepole stand, that on the southeast slope of Mount Meeker, proved to be 232 years old, indicating a probable fire in 1676.

The structure of the mature forest shows no signs of differences due to fires, even though these are separated by more than 100 years. This means, therefore, that a lodgepole forest matures in from 100 to 150 years, and after that undergoes practically no change in structure, while the trees show little increment in growth. This is supported by the condition of the 44-year forest, which is already taking on the typical closed structure, though the growth of certain trees and the elimination of suppressed ones will continue for several decades more. Physically, the mature forest has a light value quite too low for the ordinary forest species. Moreover, the competition for water between deep-rooted species and the pines is keen, though it is clear that the inability of young seedlings and of shallow-rooted herbs to grow is due to the shade. The striking absence of cover is an accurate index of the impossibility of seeding. The harvest of cones decreases gradually as the trees grow taller and the crowns compete more sharply for light. It is probable also that the number of seeds per cone is reduced as well.

CONE AND SEED PRODUCTION.[a]

So far the discussion has been confined to the effect of fires upon the forest as a whole. In order to consider fully their influence upon the forest, however, it is necessary to consider lodgepole as a tree, especially its reproduction and rate of growth.

Lodgepole pine first produces cones at varying ages, from 5 to 20 years. At Sulphur Springs, where it is much drier than in Estes Park, two 5-year seedlings were found each bearing two full-grown cones. In Mills Park the youngest cone-bearing pine found was 12 years old, and as a rule the first cones appeared in the fifteenth year. This was true of seedlings which were more or less scattered; in dense groups cones rarely appeared until several years later. Naturally, when lodgepole is badly suppressed a tree may attain an age of 50 years or more without bearing a single cone. There is no question of the close connection between the number of cones produced and the amount of water and light available, either directly or in consequence of competition.

The number of cones borne by a single adult tree ranges from none in suppressed individuals to a maximum of 9,000 in a 99-year tree in an open stand. The density of the stand is of the first importance in cone production, and with variations due to age serves to explain the most striking differences. Trees which stand alone or in open groups tend to produce the maximum of cones, owing to their large crowns. Upon mature trees in dense stands the total number of cones rarely exceeds a few hundred. In more open situations the minimum usually exceeds 2,000, and for trees from 80 to 99 years actual counts gave a range of from 2,020 to 9,000 cones. Trees 40 to 50 years old, in the open, gave a range of from 257 to 1,520 cones, and in dense stands from 0 to 64.

The number of cones has no fixed relation to the amount of seed produced. The number of seeds in a cone depends upon its size, the age of tree or branch, the number of scales, and whether each scale bears 1 or 2 seeds or none at all. The basal scales of a cone do not bear seeds, and from 3 to 6 scales at the tip are also without them. The remainder of the cone between the tip and base has few scales that are seedless. The ratio of scales to seeds varies as much

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[a] Mr. Gilbert B. MacDonald, of the Forest Service, collected most of the material used, and Mr. Carl P. Hartley, of the Office of Investigations in Forest Pathology, Bureau of Plant Industry, made the detailed study of cones and seeds upon which this account is based.

between different cones on the same tree as between those on different trees. The following table, based on 25 cones from the Targhee National Forest, shows the relation between scales and seeds:

Relation between scales and seeds (Targhee Forest).

Number of scales.	Average number of seeds per cone.	Number of scales.	Average number of seeds per cone.
71 to 80	0	121 to 130	26
81 to 90	9	131 to 140	35
91 to 100	14	141 to 150	20
101 to 110	21	151 to 160	45
111 to 120	15	161 to 170	29

These 25 cones from the Targhee National Forest showed an average of 5 scales for every seed produced. Thirty-eight other cones from the same Forest gave a ratio between scales and seeds of 5.7, and a number of cones from the Holy Cross Forest of 5.8.

The relation between the length or diameter of the cone and the number of seeds is fairly uniform, as the two tables which follow show:

Length of cone and number of seeds, based on 24 cones.

Length.		Average.	Length.		Average.
Mm.	*Inches.*		*Mm.*	*Inches.*	
21 to 25	0.8–1.0	0.5	41 to 45	1.6–1.8	23.0
26 to 30	1.0–1.2	7.7	46 to 50	1.8–2.0	43.5
31 to 35	1.2–1.4	15.5	51 to 55	2.0–2.2	46.0
36 to 40	1.4–1.6	28.2			

Diameter of cone and number of seeds, based on 18 cones.

Diameter.		Average.	Diameter.		Average.
Mm.	*Inches.*		*Mm.*	*Inches.*	
17 to 19	0.7–0.8	10.5	25 to 27	1.0–1.1	30.5
20 to 22	0.8–0.9	29.5	28 to 30	1.1–1.2	44.5
23 to 24	0.9–1.0	21.8			

The number of seeds per cone also seems to increase with the age of the cone. It is extremely doubtful, however, whether this indicates that vegetative activity continues in the cone after it reaches maturity at the end of the second year. Two other possible explanations are that the increase in the number of seeds with the age of the cones found in the course of this study was merely the result of a difference in favoring conditions when the seed was produced, or that cones with a considerable number of seeds are likely to stay on the tree longer without opening than those with fewer seeds. Neither of these explanations can be considered as final or entirely satisfactory, however, and further investigation of this point is necessary.

Age of cones and number of seeds.

Age.	Number of cones.	Number of seeds.	Average.
Holy Cross Forest.			
2 years	92	986	10.7
4 years	116	1,528	13.1
8 years	107	1,537	14.3
Total	315	4,051	12.8
Targhee Forest.			
4 years	80	1,089	13.6
Other ages	40	751	18.7
Do	19	404	21.2
Total	139	2,244	16.1

An average was also obtained from 10 trees, represented by 4 to 9 cones each. This was found to be 20.3 seeds per cone.

Variations in the number of seeds per cone and of cones per tree is shown by the above tables to be extreme. The total seed production of a lodgepole forest can consequently be estimated only in the most general way. The average number of cones on the trees counted in the Targhee Forest was 2,677, for the Holy Cross Forest 1,635. These figures indicate an average seed production per tree of approximately 50,000 and 21,000, respectively. The total seed production of a mature forest thus becomes something enormous. This has little bearing upon the reproduction, however, since both the total crop and the annual crop of seeds are important only in so far as they affect the number of seeds actually available for migration or germination each year. The periodicity of seed years undoubtedly plays a part in bringing about great variations in the total seed production. The fact that the cones remain on the trees makes it possible to obtain some evidence as to the period between maximum seed years. In spite of considerable variation from one year to another, the lodgepoles in Estes Park show little evidence of a periodic alternation of seed years, such as is often found in yellow pine and spruce.

THE OPENING OF CONES.

It is now certain that the old belief that lodgepole cones open in the forest only as a result of fire is incorrect. The cones open normally by drying out, assisted by temperature extremes. Recent observers have emphasized the point that the great majority of cones capable of opening do so immediately after maturity. Observations made in the course of this study show that the cones open normally in Estes Park after 10 to 12 years, though many open earlier. It is extremely probable, however, that cones open much more slowly in some regions than in others. As a general rule, there appear to be two periods of opening. The first period comprises several years immediately following maturity, and the second falls between the tenth and thirteenth years. Usually one of these periods will be much more marked than another in a particular region.

It seems probable that the opening of the cones between the tenth and thirteenth years is due to the fact that the pedicel breaks at about this time and makes it impossible for the cone to obtain water from the tree. As a result, the cones become much drier, and this overcomes the effect of the resin in holding the scales together. Cones fall when the pedicel breaks near the base of the cone, but they often hang on the trees permanently if the pedicel breaks at its union with the branch and is then held by the growth of tissue about it.

A test was made to ascertain whether large cones open more readily than small ones, a statement which has often been made. The following table shows, however, that practically as many large cones remain closed as small ones, indicating that size is not a factor in opening, especially if the small, completely aborted cones are excepted. The table is based upon 25 closed cones of each age, each group taken from 7 or 8 different trees:

Variation in size of closed cones.

Age.	Average length.		Number over 37 mm. (1.5 inches) long.	Number under 27 mm. (1.1 inches) long.
Years.	*Mm.*	*Inches.*		
2	34.8	1.4	11	5
6	32.5	1.3	8	2
10	32.2	1.3	6	5
12	29.1	1.1	5	10
14	32.6	1.3	8	5

Individual trees in the same stand show the most extreme differences in cone opening. In several cases a tree has been found with all of its cones opened, while beside it was a tree of the same age and size with all its cones closed. Among the trees of the same stand studied by MacDonald those older than 55 years had three-fourths of their cones closed and those below 55 years had five-sixths of their cones open. The variable behavior of trees with respect to cone opening is clearly seen in the following table:

Relation between age of trees and opening of cones.

Age.	Diameter.	Cones open.	Cones closed.	Stand.
Years.	*Inches.*			
30	6	All.	0	Open.
30	6	0	All.	Do.
30	5	38	47	Do.
39	5	0	29	Dense.
40	6	725	12	Open.
42	8	1,520	0	Dense.
45	5	2	342	Open.
55	3	64	0	Overtopped.
80	16	2,300	70	Open.
85	14	20	2,000	Do.
98	14	0	7,500	Do.
99	18	3,000	9,000	Do.
100	14	All.	0	Do.
100	14	0	All.	Do.

Cones open in consequence of the softening or disappearance of the resin which holds their scales together at the tips, and of the drying out of the scales. Heat plays a part in both cases. The action of heat alone is merely to soften the resin and to release the tips, but by increasing the dryness of the air it also acts indirectly in causing the scales to bend back. The action of heat alone is seen when cones are put in boiling water. The scales crack apart almost immediately in consequence of the softening of the resin, but they quickly close up again. If the cones are then taken from the water and dried, they open completely in a few days. They may again be closed at any time by soaking them in either hot or cold water, proving that dryness is the decisive factor in opening.

It is impossible to formulate a general rule to cover the effect of temperature upon cone opening. Individual cones behave differently. The amount of moisture present in the air and in the cones is a factor, and many temperatures insufficient to produce immediate cracking will do so after a time. In general, very few cones open completely at temperatures below 45° C. (113° F.), regardless of moisture conditions, though many open the thin scales on the lower side of the cone. In some cases cones which showed no effect at first begin to crack several hours or even several days later, suggesting that the moderate temperature may ultimately have a chemical effect upon the resin. Water or moist air at a temperature capable of cracking a cone in an hour will crack it more quickly than dry air at the same temperature. All or nearly all the scales on the great majority of cones will crack open at from 45° to 50° C. (113° to 122° F.), while temperatures above 50° C. (122° F.) open most cones promptly. A temperature of 69° C. (156° F.) will crack open almost all cones immediately. No temperature below 40° C. (104° F.) proved sufficient to open cones. Those which failed to open below 45° C. (113° F.) showed no change from longer treatment at the same temperatures, even when continued for two weeks.

After the scales had cracked apart it was found that moist heat did not cause them to spread. Dry heat also had no effect, except when the cone contained much moisture. The rapidity with which a cone is dried determines the degree to which the scales will open. Cones rarely spread their scales sufficiently to loosen many seeds at a single drying. They must again be moistened and dried, when the scales will separate still farther and loosen additional seeds. This takes place in the woods with cones exposed to several rains with intervening dry periods, and the gradual shedding of the seeds explains in part the slowness of reproduction in those areas where the animal population is large.

From what has been said it is clear that the effect of fire in opening cones of lodgepole pine consists in burning off the resin and then drying out the scales. Fire will fail to open cones which are very dry, and cones which remained closed throughout a fire may continue to open for years afterwards with the alternation of dry and wet periods. The cracking apart of the scales under normal conditions seems to be due largely to the fact that the resin is more easily acted upon by heat when the cones are just mature. The breaking of the resin from the tenth to the thirteenth year and after is best explained by the gradual effect of weathering and in some degree by a chemical change in the resin. Resins break down in the presence of an alkali into nonadhesive substances, and it is probable that rain water trickling over the bark might in the course of years exert this action. The action of water alone is slight, since cones continuously immersed in tap water for over six months showed no effect, but the presence of water in connection with heat and cold affords the most plausible explanation of the removal of the resin. In a region where the humidity is extremely low and rains frequent, the final complete opening of the cones in consequence of the bending of the scales needs no further explanation.

The probable effect of fire upon seeds was studied in connection with the artificial opening of cones. Four-year cones from the Targhee Forest were used. The experiment was checked by the use of seeds from cones which had been opened mechanically.

Effect of temperature upon germinability.

	Total seeds.	Number germinated.	Percentage.
Check, mechanically opened	101	3	3.0
Water at 60° C. (140° F.), 40 minutes	271	37	13.7
Water at 80° C. (176° F.), 20 minutes	278	3	1.1
Flame of Bunsen burner, 10 seconds	172	16	9.3
Flame of Bunsen burner, 30 seconds	120	6	5.0
Flame 30 seconds, but cone allowed to burn out, usually requiring 1 to 2 minutes	85	2	2.4

This single experiment is suggestive rather than conclusive, though it does show conclusively that some seeds survive a fire which would burn off the ends of all the scales. Cones held in the flame were completely cracked open in less than 10 seconds, and had caught fire in 20 seconds. The cones which were allowed to burn out had their scales charred for a considerable distance back from the tip.

DISTRIBUTION OF CONES AND SEEDS.

In spite of its winged seeds, the extension of lodgepole is necessarily local and slow. The agents of seed distribution are wind, gravity, water in the form of surface drainage and streams, and animals, especially squirrels, chipmunks, and birds. The conditions which govern distribution and germination are so different in the living forest and in a burn that it is necessary for the sake of clearness to consider them separately. After the normal forest is once established, in about thirty years, distribution is of practically no value unless seed or cone is carried out of the forest. With the exception of wind the agents named carry the cones and seeds only a short distance from the edge of the forest. Even with wind the distance was never found to exceed 50 meters (164 feet). Brooks were found to carry seeds and cones farther, but as a rule they destroy the power of germination. Roll and surface wash carry cones away from the parent trees for a short distance, but play a negligible part in the living forest.

Squirrels and chipmunks, and to a less degree birds, are the factors which have the greatest influence upon seed distribution. As is well known, the distribution they effect is in connection with the gathering of cones and seeds for food. So far all the evidence shows that their action as food gatherers makes extension of the forest practically impossible. This is due chiefly to the completeness with which they harvest the crop of cones, but it also arises from the fact that they make their homes for the most part within the forest. Consequently they serve to carry the cones at the forest edge deeper within the forest, where reproduction is impossible. No figures are available as yet which show what proportion of each cone crop is carried off by squirrels and chipmunks. Convincing evidence has repeatedly been found, however, that the number of 2-year cones which they gather each year is large enough to prevent extension. At certain times of the summer the forest floor is found thickly strewn with twigs, usually bearing fresh cones, but sometimes also cones several years old (Plate VI, fig. 2). Many of these cones are "shelled" on the spot, but most of them are carried away to some central place where they are gnawed apart. The mass of old scales is many feet in extent, and from 1 to 2 feet deep. In all such places not a single seed was found to have been overlooked. In fact, no separate seed of either lodgepole or limber pine was found in the forest, and only rarely does a seed lurk in an open cone on the ground. For the lodgepole forests of Estes Park, the conclusion seems inevitable that squirrels and chipmunks, with the help of the jays, not only carry off the larger share of the fresh crop of cones each year, but also secure practically all the seeds which fall as the older cones open from time to time.

Distribution after a burn is essentially simple, since the seeds fall for the most part beneath or near the parent trees. Yet pure lodgepole stands have usually arisen from mixtures, and have been made possible only by the movement of seeds and cones away from the parents. In this, wind, roll, and wash have all been active and serve to explain the actual differences in grouping shown in various parts of a burn. The most important thing, however, is to explain the part taken by the rodents. The striking reproduction in burns as compared with the complete absence of seedlings in clearings and other suitable areas seems to admit of but one conclusion, namely, that the difference is due to the absence of squirrels and chipmunks in the burns. A forest fire will kill a large number of squirrels and chipmunks and drive many, if not all, of the survivors away. The chipmunks would return first, but they could hardly become abundant for several years, owing to the sparse food supply. The squirrels would not become numerous again until the new trees had begun to bear cones plentifully. As a matter of fact, in forests less than 40 years old, no squirrels were seen. The almost complete absence of rodents for at least two or three years after a fire explains the typical reproduction of a burn. It also makes it clear that areas in which the seed production and conditions of water and light are favorable are destitute of seedlings because the seed crop is practically all taken by the rodents which make their home in the forest. It also indicates that the burning of cut-over areas to insure reproduction owes as much of its success at least to driving out the seed-eating animals as it does to insuring the proper physical conditions.

THE GERMINATION OF SEEDS.

Germination in cultures.

Series.	Forest.	Age of cones.	Number seeds.	Number germinated.	Percentage.
		Years.			
1			65	22	34
2			157	81	52
3			104	32	31
4			480	193	40
5	Holy Cross		241	128	53
	Targhee		298	81	27
6	Holy Cross	2	81	33	41
	Targhee	2	108	47	43
7	Holy Cross	6–11	118	75	54
	Targhee	6–11	32	7	22
8	Holy Cross	16–18	42	20	48
	Targhee	16–18	49	8	16
9	Holy Cross		121	71	59
	Targhee		91	22	24
10	Holy Cross	2	127	74	58
	Targhee	2	137	52	28
11	Holy Cross	6–9	130	79	61
	Targhee	6–9	32	7	22
12	Holy Cross	11–12	63	26	41
	Targhee	12–14	30	4	13
13	Targhee	2	280	101	36
		3–5	46	11	24
		7–9	32	7	22
		12–14	71	14	20
		16–20	116	25	22
		23–25	30	6	20
		41	20	0	0
14	Holy Cross	All ages	362	199	55
	Targhee	All ages	626	184	29
15	Holy Cross, dead tree in burn	6–8	25	18	72

Germination in sandy soil.

Series.	Forest.	Age of cones.	Number seeds.	Number germinated.	Percentage.
		Years.			
1	Holy Cross	18	59	16	27
2	do	25–26	41	12	29
3	do	45–50	23	3	13
4	do	75–80	39	3	8
5	Targhee, large cones	2	187	13	7
6	do	12	140	1	0.7
7	do	18	150	0	0
8	Targhee, small cones	2	35	9	26
9	do	6	50	7	14
10	do	12	81	3	4
11	do	18	57	5	9
12	do	25–26	80	2	3
13	do	37+	73	0	0
14	Holy Cross	18–27	100	28	28
	Targhee	18–27	287	7	2
15	Targhee	2–26	780	40	5

From the preceding table, it is evident that seeds from the Holy Cross Forest germinated much more successfully than those from the Targhee Forest. For the former the percentage for seeds of all ages was 55, for the latter 29.5. Seeds from the Targhee Forest germinated nearly 50 per cent better at maturity than at from 3 to 5 years and later. Beyond 5 years, there appeared to be little loss in viability, even in cones 25 years old. Seeds from the Holy Cross Forest germinated as well or even better when several years old as at maturity, though a falling off was apparent at from 12 to 14 years. The percentage of germination of Colorado seeds less than 10 years old, in Petri dishes, was practically the same as that secured by the seed laboratory at Washington. The percentage obtained for seeds more than 10 years old was much lower, however, but this was in all likelihood partly due to the small number of older seeds available for the present study. Most of the germination cultures were kept alive for only eight weeks, instead of fourteen as in the Washington experiments, and this doubtless reduced the percentage somewhat. On the other hand, practically all of the seeds used were soaked in water or in a dilute solution of formalin before being put into the plates. This hastened germination, and counterbalanced in a large measure the effect of the shorter life of the culture.

The seeds from each cone were kept separate throughout the tests. It was found that seeds from different cones showed great variability in germination. Seeds from ten 2-year cones from the Targhee Forest showed 55, 50, 33, 17, 27, 21, 47, 0, 34, and 31 per cent, respectively. Of these cones the five containing more than 17 seeds averaged 37 per cent of germination, while those containing less than 17 seeds averaged 30 per cent. This difference in the viability of seeds from cones containing many and few seeds appeared to be general. Though there is little difference in size between the seeds of any one cone, the seeds of different cones vary greatly. The 35 seeds of cone 16 averaged 44 milligrams (0.7 grain) each, while the 19 seeds of cone 25 averaged but 16.5 milligrams (0.3 grain). It was found that 299 seeds from the Targhee Forest averaged 28.9 milligrams (0.4 grain), and 224 seeds from the Holy Cross Forest 29.2 milligrams (0.5 grain). No apparent relation was discovered between the weight of the seeds in various cones from the Targhee and their germination. In one series of germination comprising nine cones less than 20 years old from the Holy Cross Forest, four cones had seeds weighing more than the average and five had seeds weighing less. The heavier seeds averaged 62 per cent of germination (per cone 57, 52, 72, and 62 per cent, respectively) and the lighter seeds 39 per cent (33, 38, 45, 43, and 38 per cent, respectively). These results from the two Forests are diametrically opposed. They indicate some important difference in actual conditions, connected probably with the much lower viability of seeds of all ages from the northern forest.

The table also gives the results of the germination of seeds of different ages from both Forests. These were planted May 31 in sandy loam in pots in the greenhouse, and were later put out of doors. The results were more variable than those from the Petri-dish tests. The percentages were not only much lower than those obtained from the Petri dishes, but also lower than the results obtained in nursery tests made by the Forest Service. The Idaho seeds again did not behave as did the Colorado seeds in nursery tests, for the germination of seeds less than ten years of age was greater than for seeds over ten years. Four plantings made in the open gave the following results:

1. Two thousand seeds were planted May 12 in sandy loam beneath the shade of cottonwoods. The ground was cold and wet. The seeds germinated very slowly, and only a very small number of plants developed.

2. One thousand seven hundred seeds were planted May 16 in very sandy soil in the open. Germination was fairly rapid, as the weather after planting was warm and moist. On July 9, 354 seeds, about 21 per cent, had germinated. Few seedlings appeared after this date.

3. Part of the plot beneath the cottonwoods was replanted on June 26. A few seeds only of this planting germinated.

4. On June 26, seeds were planted in open rich soil, and in fairly dense hardwood forest near Lake Minnetonka, Minnesota. No seedlings had appeared in either place as late as September 1.

The best results obtained here fell below those secured in the nursery experiments of the Forest Service. It is probable that all the plantings were made too late for the best results. All the seeds planted in pots or out of doors were first soaked. Most of the seeds used were 2, 4, and 8 years old, and from the Holy Cross Forest.

The soil was exceptionally wet until the middle of July, and in the late summer exceptionally dry, facts which explain in part the poor results obtained.

The most remarkable fact discovered during this work was the germination of three seeds from each of two cones. One of these was known to be 45 years old, and the other over 75 years. The slowness of germination of some seeds is also a matter of much practical importance, and has a direct bearing upon one-year differences between seedlings in burns. Many seeds required three months for germination, while some germinated after nearly five months had elapsed.

The seedlings which appeared in the different plantations on the University of Minnesota campus were observed during the summer in the hope of determining their adaptability to Minnesota conditions. The extraordinary nature of the summer, however, rendered the results of little value. Of the seedlings from the plantings of May 12 and June 16 in the cottonwood plot, 19 were alive on October 7. This number is approximately 25 per cent of the total number of seedlings that appeared on the plot. The seedlings tended rather unaccountably to appear in particular patches, a fact also true of the open plots. Of the 354 seedlings at one time counted on the open sandy plot, only 9 were found on October 7. Seedlings died steadily throughout the summer, usually in groups of 12 to 15 at a time, scattered rather uniformly over the entire bed. Germination was much more prompt and complete here than in the shade, but the gradual browning of the seedling patches has progressed steadily. On August 15, a lath shelter was placed over half of the plot in the open, reducing the direct sunlight two-thirds. Of the 9 seedlings remaining, 6, all of them the healthiest, were found to be outside the shaded area.

In nature, young seedlings of a year or less in age were found so rarely that no conclusions whatever can be drawn from them. A single quadrat in the 28-year burn yielded 25 seedlings a year old, but this was as great as the total number of seedlings of this age throughout all other areas studied. The success of natural germination in burns can be conjectured from the reproduction in recent burns. It will be impossible to determine this relation with accuracy until a burn can be studied for the first two or three years of its history.

RELATION OF DEVELOPMENT AND GROWTH TO LIGHT AND WATER.

The growth and structure of lodgepole pine are determined by the three direct factors—water, light, and temperature. Because of its greater daily and seasonal variations, the effect of the last is the least evident and probably the least important. The necessary adjustment of the individual to these has made it possible for the species to cover a wide range of latitude and altitude. In consequence it is difficult to distinguish any essential difference in the development of trees at altitudes from 400 to 600 meters (1,300 to 2,000 feet) apart in spite of noticeable differences in temperature. With water and light, however, the case is very different. The action of light, especially in the case of seedlings, is much the more marked, but differences in water content also produce important effects. In many cases, the effects of light and water are so merged that it is impossible to distinguish between them. This difficulty becomes extreme when the individuals enter into competition with each other, or with the herbaceous plants which form the ground cover. In all cases, lodgepole is less able to adjust itself to variation in light than to variation in either water content or temperature. This fact indicates almost conclusively that light is more decisive than water, whether competition is present or absent.

The optimum light for lodgepole at all stages of development is sunlight. Seedlings will develop and suppressed trees maintain themselves in light much weaker than ordinary sunlight. The amount of reduction in light intensity which lodgepole can withstand is smaller than in any of its associates. The light values in mature forests range from 0.12 to 0.05; the values most frequently found were 0.08 and 0.07, which may well be taken as the normal. At intensities of 0.2 to 0.14 germination and growth are fairly good, though much below that in sunshine. They fall off markedly from 0.14 to 0.1, and practically cease below the latter. The increase in height with respect to diameter rises steadily as the light intensity falls from 0.2 to the lower limit. No vigorous seedlings were found in forests with light values from 0.08 to 0.05, and seedlings of any sort were very rare. The weakest light found in the lodgepole forest, 0.016, occurred in a dense thicket-like group in which there was no ground cover, and represents the normal minimum for the denser grouping of lodgepole pines.

With the exception of the aspens, the normal light intensity of the forests which touch the lodgepole areas is as a rule considerably lower. The light intensity in the denser aspen forests ranges from 0.04 to 0.08, with the normal at 0.05 to 0.06. These values readily explain the inability of lodgepole seedlings to maintain themselves in aspen. Yellow pine rarely gives a continuous shade in this region, and hence need not be taken into account, though it is interesting to note that the light value of the shadow cast by the crown is the same for both species. The light intensity in the stands of limber pine is approximately the same as that in the mature lodgepole forests, though because of the more irregular grouping of the trees it is usu-

FIG. 1.—EFFECT OF COVER COMPETITION IN A STANDING BURN.

[The two seedlings were neighbors, the larger in a bare spot, the smaller in a carpet of *Vaccinium*.]

FIG. 2.—FOREST FLOOR STREWN WITH CONE-BEARING BRANCHES CUT OFF BY SQUIRRELS.

ally much less uniform. Where Douglas fir predominates, and in the Engelmann spruce-fir type, the light intensities are uniformly lower than in the lodgepole areas. Typical intensities range from 0.04 to 0.02, and in the older mature forests the values fall below 0.01. It is very significant that lodgepole seedlings are the only ones which are unable to endure any of the intensities given above. The tolerance of limber pine seems to be only slightly greater, but the infrequency with which its seeds escape birds and rodents made it impossible to determine this accurately. Douglas fir grows readily under lodgepole shade of from 0.1 to 0.05. Below this it rarely thrives in Estes Park, though it grows fairly well in light of 0.02 at Pikes Peak. Engelmann spruce and alpine fir are almost identical in their tolerance. No forest light measured was too weak for fair reproduction of both species. As a rule they occur side by side, but the range of the spruce is wider and its seedlings are more abundant. This is doubtless due to its reproducing by seeds, while all the young firs examined had started by layering from the lower branches of parent trees.

The summer of 1907 was fairly uniform in rainfall, while that of 1908 was unusually dry until after the middle of July. This made it possible to determine the average or normal water content, and the extremes as well, especially under conditions approaching drought. The building of a new dam by a colony of beavers also afforded an excellent opportunity to observe the effects of an excessive water supply. As might have been expected, the trees in the shallow pond, about 1 foot deep, were rapidly turning brown and dropping their leaves. It was more significant that this effect, though more gradual, was scarcely less apparent along the borders of the pond, where the soil was saturated. This tallies with the fact that the highest water content in which perfectly healthy lodgepoles were found growing was 34 per cent, and that seedlings and adult trees were uniformly absent in soils with from 35 to 50 per cent of water. In 1907, the water content values for lodgepole forests in Mills Park ranged from 7 per cent to 25 per cent. The most frequent values were between 8 per cent and 10 per cent. At Sulphur Springs, where the abundance of sagebrush indicates a much drier climate, the water content of the lodgepole forest varied from 5 per cent to 8 per cent. During the first half of the summer of 1908, the water content of lodgepole habitats in Mills Park was unusually low, ranging from 2.5 per cent to 8.9 per cent. Water values of 3 per cent and 4 per cent were often found, especially on the steeper slopes, and the average of all the determinations made during this period was only 5.5 per cent. These lodgepole soils, however, are typically gravel with relatively little humus. In consequence, the nonavailable water is very low, always less than 1 per cent, and in the coarser gravels, about one-half of 1 per cent. From this it is evident that a gravel soil with 2.5 per cent of water is far from dried out, and one with from 5 to 6 per cent is in fairly good condition. During the latter half of the summer the water content was much higher. The minimum content found in gravel during this period was 10.4 per cent, the maximum 15.2 per cent. In the 200-year forest, where there was much needle mold, values of 22 to 25 per cent were found. In such soils about 5 per cent of the total water content is nonavailable. The average of all the samples taken during this wet period was 14.7 per cent.

The water content of the other forests which touched the lodgepole areas was uniformly higher. It was highest in the aspens, which showed from 14 to 20 per cent when the adjacent lodgepole soils contained only from 5 to 7 per cent, and, later in the summer, from 25 to 40 per cent, in comparison with from 10 to 15 per cent in the lodgepole. The ability of aspen suckers to take possession of the ground after a fire, and of the mature trees to hold it against the invasion of the pines, is largely due to this higher water content, which is distinctly unfavorable to lodgepole. The mixed forests of Douglas fir and lodgepole as a rule show water contents of few degrees above that for the pure lodgepole stands, though no greater than for the mature lodgepole forests. Likewise the mixed zone of Engelmann spruce and alpine fir shows a constantly higher water content, ranging from 15 to 30 per cent. These two conifers grow best in water contents equal to those found in the aspens, though the zone in which they thrive is usually well above that in which the aspen reaches its characteristic development. These three species when they meet the lodgepole in anything like equal numbers will crowd it out in the moist soils, and yield to it in the dry ones.

In this region limber pine has a wider altitude and range than lodgepole, and while its moisture requirement is usually somewhat greater it is sometimes associated with yellow pine in areas which are normally too dry for lodgepole. Douglas fir requires a slightly higher water content, but at the lower altitudes it thrives equally with lodgepole in values of from 12 to 15 per cent.

RELATION OF REPRODUCTION TO COMPETITION.

All of the evidence obtained in the present study indicates that competition is wholly a question of available water and light. In exhausted soils and those poorly aerated, both nutrient salts and air play a part in competition. In natural habitats, however, such as those of the lodgepole forests, where all the nutrient salts taken from the soil are ultimately returned to it, and where the loose texture of the gravel permits thorough aeration, these factors are negligible.

Competition in all such places is narrowed to the question of the total amount of water and light present, and the amount of each available for any particular individual in consequence of the presence of neighboring individuals. In many cases of competition there can be no doubt that the amount of both water and light available for a competing group is less than the normal development requires. Competition is then for both water and light, and often in more or less equal degree. The latter point will naturally depend upon the total amount of available water or light present in relation to the amount actually required by each plant. In the majority of cases, however, while the total of either factor is inadequate, the deficiency is greater in the case of one than of the other. The same result is obtained when the size, the form, or the arrangement of the individuals is such that they react upon one factor more than upon another. This is typical of lodgepole communities. The seedlings have little or no effect upon the light available for each until they have attained a height of 1 or 2 meters (1 or 2 yards), and then only when they are unusually crowded. On the other hand, they compete vigorously for water whenever the roots enter the same area. Owing to the usual density of seeding, such competition is the rule in all recent burns, especially since the water content is relatively low. While this competition becomes more keen as the seedlings develop into adult trees, the inability of lodgepole to stand any material reduction of light intensity seems to give paramount importance to competition for light in all stands above 20 years of age, This must be understood to apply only to stands dense enough to bring the individuals into competition with each other.

The nature and the intensity of the competition also depends upon the group of individuals concerned. Competition may exist between the cover and the seedlings in it, or between the seedlings, or the adult trees themselves. In the first case, the process is complicated by the fact that seedlings may often stand so thickly in a dense cover that they compete with each other as well as with the species of the cover itself. It is fairly well established that competition is keenest between individuals of the same species, because they make essentially the same demands upon the habitat. Competition decreases steadily as species are more unlike in ecological form and behavior, and disappears altogether when one species becomes dominant, as in the case of a tree and the tiny annual that grows beneath it. With lodgepole, the keenest competition will occur where the herbaceous ground cover still persists and where seedlings are sufficiently crowded to compete with each other. Since competition varies directly with density, it is often most marked in extremely dense stands from which the ground cover has long since disappeared. The effect of a compact cover upon scattered seedlings is clearly evident as a rule. The relations between lodgepole and its tree associates are based largely upon light requirements, and, as will be shown later, depend chiefly upon the rate of growth.

The effect of cover competition upon the growth and form of lodgepole seedlings shows most strikingly in the dense carpets of Vaccinium. It is apparent in some degree with other species of the herbaceous cover, but is rarely marked. The first effect of the blueberry is to reduce the light available for the year-old seedlings, but its chief effect is exerted through the reduction of the available water. During the first few years the roots of both species occupy essentially the same soil layer, with those of the blueberry as a rule deeper. A count of the seedlings of 40 centimeters (15.7 inches) and over on two 10-meter quadrats in a standing burn gave the following results:

Needle mold.			Rock edge.			Vaccinium cover.		
Number.	Height.		Number.	Height.		Number.	Height.	
	Cm.	*Inches.*		*Cm.*	*Inches.*		*Cm.*	*Inches.*
2	40	15.7	1	40	15.7	1	45	17.7
1	41	16.1	1	41	16.1			
3	42	16.5	1	42	16.5			
1	43	16.9	1	44	17.3			
1	45	17.7	1	45	17.7			
1	47	18.5	1	46	18.1			
1	48	18.9	1	48	18.9			
1	50	19.7	2	50	19.7			
1	55	21.7	1	52	20.5			
1	57	22.4	2	55	21.7			
			1	56	22.0			
			1	58	22.8			

With these figures may be compared those obtained by the random measurement of 30 seedlings from a Vaccinium patch:

Number.	Height.		Number.	Height.		Number.	Height.		Number.	Height.	
	Cm.	*Inches.*		*Cm.*	*Inches.*		*Cm.*	*Inches.*		*Cm.*	*Inches.*
1	7	2.8	1	13	5.1	3	18	7.1	4	22	8.7
1	9	3.5	3	15	5.9	1	19	7.5	1	24	9.4
1	10	3.9	1	16	6.3	4	20	7.9	2	27	10.6
1	11	4.3	3	17	6.7	1	21	8.3	1	[a] 40	15.7
1	12	4.7									

[a] Rock.

The average of the plants in the Vaccinium cover is less than half that of those in the same quadrat unaffected by competition. The effect upon the plant as a whole is seen in Plate VI, figure 1, which shows two representative plants, the smaller from the Vaccinium carpet, the other from a bare spot near by. The average diameter of the seedlings within the Vaccinium was 7 millimeters (0.28 inch), of those outside 12 millimeters (0.47 inch). The height growth of seedlings under competition was from 5 to 7 centimeters (2–2.8 inches) in 1907 and the same in 1908. The growth of seedlings not in the cover was from 12 to 14 centimeters (4.7–5.5 inches) in 1907 and from 15 to 17 centimeters (5.9–6.7 inches) in 1908. Almost without exception the largest seedlings were found at the lower edge of a rock. The more rapid growth in such places is doubtless due to the action of the rock in preventing the growth of competitors on one side and in increasing the amount of available water by checking run-off and by preventing evaporation from the soil covered.

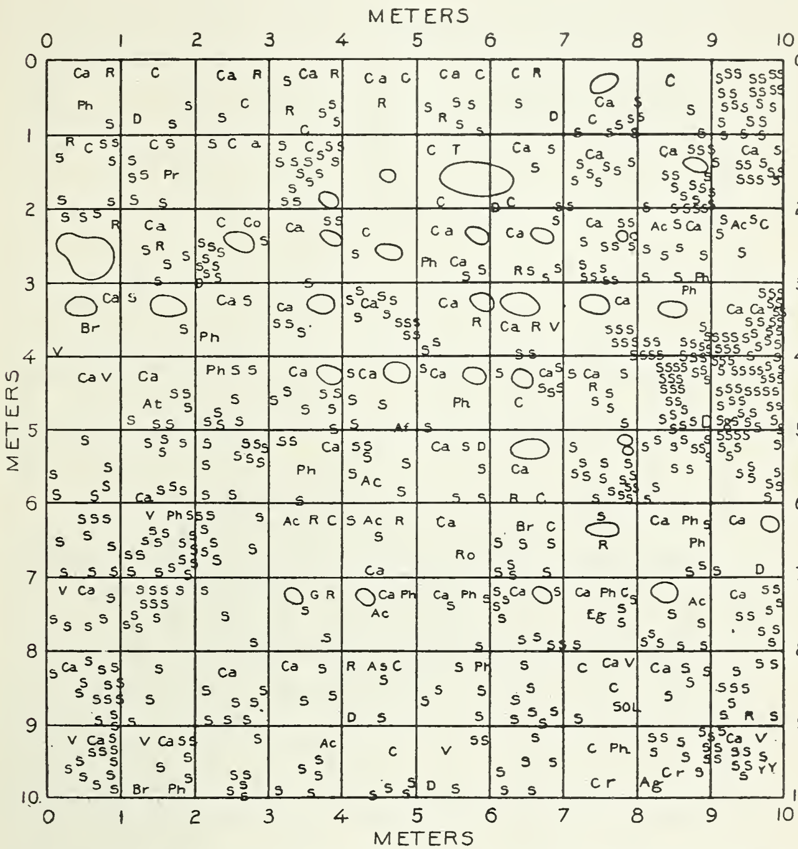

Fig. 1.—Sample quadrat, showing seedlings and cover in a half-burned area. S=seedling lodgepoles; C=*Chamænerium; angustifolium;* V=*Vaccinium oreophilum;* Ca=*Carex rossii;* R=*Rubus strigosus;* Ph=*Phacelia lyallii;* Ac=*Achillea lanulosa.* All quadrats 10 meters square.

The effects of competition between individuals, due to density of stand, are clearly shown in figure 1. In these quadrats, the density is more than 1,000 individuals to the 10-meter quadrat, or 10 to the square meter (1.2 square yards). In the mature forest of the usual type, the density is about 20 trees per 10-meter quadrat, or 1 tree to every 5 square meters (6 square yards). The ratio between normal density and maximum density is consequently about 1:50. The relative competition in the two areas can not even be estimated at present, since we have no quantitative expression for any of its terms, apart from the gross effect upon light intensity and upon water content. The final outcome in so far as growth is concerned is indicated by the following table, which shows the height and diameter of individuals under the most intense competition. The majority of these were from 38 to 43 years old, though a few were less than 30 years.

Height.		Diameter.		Height.		Diameter.		Height.		Diameter.	
Meters.	*Feet.*	*Mm.*	*Inches.*	*Meters.*	*Feet.*	*Mm.*	*Inches.*	*Meters.*	*Feet.*	*Mm.*	*Inches.*
3.5	11.5	70	2.8	2.0	6.6	30	1.2	1.5	4.9	13	0.5
3.5	11.5	65	2.6	2.0	6.6	20	.8	1.4	4.6	15	.6
3.0	9.8	70	2.8	1.7	5.6	20	.8	1.3	4.3	12	.5
3.0	9.8	50	2.0	1.6	5.2	10	.4	1.2	3.9	11	.4
3.0	9.8	45	1.8	1.5	4.9	18	.7	1.0	3.3	10	.4
3.0	9.8	35	1.4	1.5	4.9	15	.6	0.9	3.0	10	.4
2.5	8.2	22	.9								

In these the minimum height was one-fourth the maximum, the minimum diameter one-seventh the maximum. This brings out clearly the fact that under competition for light, height growth is made at the expense of growth in diameter. In cone production the effect of intense competition is even more marked since the great majority of suppressed trees bear no cones whatever. No suppressed tree was found, however, on which a recognizable ring of wood was not formed each year that the tree remained alive.

With the possible exception of yellow pine, of all species of trees in the park lodgepole is the least tolerant of shade. The outcome of the competition that arises whenever it is associated with any of the other species depends largely, and in some cases wholly, upon the relative rate of growth. From the evidence of two seasons' study, lodgepole when within its normal range grows more rapidly from the first than any of the conifers associated with it. On the other hand, aspen outstrips it for the first decade or two, especially when the latter arises from root suckers. By the twentieth year, however, lodgepole overtakes the aspen, and, except in the wetter places, grows more rapidly. Aspen, therefore, will hold any place just burned, provided it can take complete possession of the ground at the very beginning. If the ground becomes too dry its growth will be retarded, and some trees gradually drop out to be replaced by lodgepole. Aspen has no value as a "nurse" growth for the pine, but on the contrary its presence retards or completely prevents the development of a lodgepole forest.

In growth and in power to compete, lodgepole, yellow pine, and Douglas fir are sufficiently alike to make fairly stable mixed forests. Douglas fir is the most tolerant of the three, while lodgepole is far superior in its ability to reproduce after a burn. In an undisturbed forest of the three the tolerant, long-lived fir slowly replaces the pines as they drop out through overshading or old age. After a fire lodgepole reappears to the practical exclusion of both fir and yellow pine. In a protected region the mixed forests will be slowly replaced by fir forests; in a fire-swept one they will be quickly replaced by lodgepole. At the upper edge of its belt lodgepole finds itself in competition with Engelmann spruce and alpine fir, both of which are much more tolerant, and at the higher altitudes much more rapid in growth. Where the three species appear the immediate outcome depends upon the amount of reproduction and the conditions for growth. Where the latter are not too unfavorable lodgepole takes possession in the usual way, but it gradually yields as the trees become sufficiently crowded to compete for light. This is chiefly the result of its intolerance, but partly of its shorter life, at least as compared with spruce. Even where lodgepole has secured a start over the other species its inability to endure its own shade causes it to yield slowly to the spruce and fir wherever these are numerous.

The almost total lack of reproduction in limber pine makes it difficult to determine its power of competing with lodgepole. Its greater tolerance and longer life enable it to maintain itself in pure forests, especially near timber line, but too few seedlings were found to determine with certainty its behavior in competition during reproduction.

RELATIVE RATE OF GROWTH.

The rate of growth is determined by three factors—the inherited habit of the species, the nature of the habitat in terms of physical factors, and the kind and degree of competition. It has been difficult to secure accurate data in regard to the habit of growth of each tree species, since these have been studied chiefly where they meet the lodgepole, that is, at the edge of or completely outside their natural habitat. The measurements obtained are somewhat contradictory, and at present it is only possible to say that in most situations throughout its wide altitudinal range lodgepole pine surpasses the other species in rapidity of growth. At its upper limit it is excelled by Engelmann spruce and fir, but here the absolute rate of growth is less than in the typical lodgepole areas lower down, with their longer growing season.

Lodgepole prefers relatively dry soils, and aspen, its most constant competitor, relatively moist or wet soils. The light requirements of both trees are great, though aspen is the more tolerant. In consequence, a comparison of field results must recognize that both physical habitat and competition have played a part in growth, and that it is impossible to separate the effects of the one from those of the other. If a comparison is made between the new individuals in the 1902 burn, it is evident that the aspen has grown much more rapidly during the first seven years. The optimum growth for 7-year aspens ranges from 1.8 to 2.8 meters (5.9–9.2 feet) in height and from 3 to 4 centimeters (1.2–1.6 inches) in diameter. The average height is 2.5 meters (8.2 feet) and the average diameter 3 centimeters (1.2 inches). The optimum growth for 7-year lodgepoles ranges from 0.5 to 0.7 meters (1.6–2.3 feet) in height and from 1.3 centimeters to 2.5 centimeters (0.5–1.0 inches) in diameter. The average pine seedling is about 0.5 meters (1.6 feet) by 1.7 centimeters (0.7 inches). The average yearly growth of aspen for this period is 34 centimeters (13.4 inches), for lodgepole about 7 centimeters (2.8 inches), or little more than one-fifth the rate for aspen. This difference is due chiefly to the origin of aspen from root sprouts, which insures an early start after a fire, and also a large supply of nutrition from the roots of the parent tree. These facts explain clearly why the lodgepole is unable to get a start in burned areas which have been occupied by aspen, and why it is unable to enter after the aspen sprouts have secured the first chance at the sunlight.

The later behavior shows that this difference in rate is not a permanent characteristic of the aspen as a species. The maximum size of aspens of 18 to 20 years growing in a loose mixture was 3.5 meters (11.5 feet) by 5 centimeters (2.0 inches), of lodgepole of the same age 3.6 meters (11.8 feet) by 10 centimeters (3.9 inches). In the burn of 1878, where the aspens and pines are as a rule 28 or 29 years old, the dominant aspen trees of the stand range from 3.4 meters (11.2 feet) by 5 centimeters (2.0 inches) to 4.9 meters (16.1 feet) by 8 centimeters (3.1 inches), with the average about 4 meters (13.1 feet) by 6 centimeters (2.4 inches). With lodgepole the variation is from 4 meters (13.1 feet) by 11 centimeters (4.3 inches) to 5 meters (16.0 feet) by 15 centimeters (5.9 inches), with the average about 4.3 meters (14.1 feet) by 12 centimeters (4.7 inches). The rate of growth in height has now become almost the same, with a slight advantage for the lodgepole. The growth in diameter is practically twice as great for the pine. The largest aspens found in the burn of 1864 vary from 5.5 meters (18.0 feet) by 6 centimeters (2.4 inches) to 6 meters (19.7 feet) by 16 centimeters (6.3 inches), averaging about 5.7 meters (18.7 feet) by 11 centimeters (4.3 inches). The corresponding lodgepoles range from 6 meters (19.7 feet) by 12 centimeters (4.7 inches) to 8 meters (26.2 feet) by 23 centimeters (9.1 inches), with the maximum at 9.7 meters (31.8 feet) by 30 centimeters (11.8 inches). The average is about 7 meters (23.0 feet) by 16 centimeters (6.3 inches). In these forests the aspen is regularly overtopped by the pine. The outcome of the competition is decided, and the final result is that the aspen is practically eliminated between the fiftieth and sixtieth years of the normal forest. The average height growth for the pine has been 16 centimeters (6.3 inches) for the period of 43 years and 13 centimeters (5.1 inches) for the aspen. The pine has averaged nearly 4 millimeters (0.2 inches) in diameter, the aspen a little more than 2 millimeters (0.08 inches). The average growth in height for the lodgepole has been almost 20 centimeters (7.9 inches) per year for the last 15 years, while for the aspen it has been but 11 centimeters (4.3 inches). No aspens cut were found to be over 49 years, at which they have reached a size of 6 meters (19.7 feet) by 12 centimeters (4.7 inches). This must indicate closely the normal limit of their life in mixture with lodgepole in the habitat of the latter. The oldest lodgepole examined was 232 years old. It stood in a normally dense stand and measured 12.2 meters (40.0 feet) by 24 centimeters (9.4 inches). Other trees in similar stands ranging from 185 to 200 years were found to be from 14 to 18 meters (45.9–59.1 feet) high. The largest lodgepole found was 20 meters (65.6 feet) high and 46 centimeters (18.1 inches) in diameter. It was 210 years old and grew in the wet soil of a brook bank, showing the possibilities of adapting the lodgepole to rich, moist soils.

It seems undesirable to attempt definite comparisons between the rate of growth of lodgepole and that of other conifers. A number of figures are available, all showing the greater vigor of lodgepole. When it is recalled that the best development of yellow pine and Douglas fir is below the lodgepole zone and the normal growth of Engelmann spruce and alpine fir above this zone, it is impossible to go beyond the statement that the lodgepole excels all its coniferous associates in its rate of growth in its own zone. It is a striking fact, however, that the yellow pine has grown only about half as fast as the lodgepole on slopes burned over in the fire of 1879. The growth of the Douglas fir is only a little less rapid than that of the lodgepole where they do not compete, but in mixed copses of the two it often grows much less than half as rapidly. Engelmann spruce regularly grows less rapidly when well within the lodgepole zone, and considerably more rapidly between 10,000 and 10,500 feet, where lodgepole reaches its limit. The alpine fir grows less rapidly after a fire than the spruce with which it is associated, in some quadrats growing scarcely half as fast. It is the most tolerant of the conifers in the park, and consequently grows better in moderate or deep shade than any of them.

Differences in the rate of growth of lodgepole seedlings due to altitude are pronounced. Above 10,000 feet, pines from 9 to 13 years old were found to be from 21 to 30 centimeters (8.3–11.8 inches) tall and from 6 to 8 millimeters (0.24–0.31 inches) in diameter. From 9,000 to 9,500 feet, seedlings of from 5 to 7 years ranged from 20 centimeters (7.9 inches) by 6 millimeters (0.24 inches) to 50 centimeters (19.7 inches) by 12 millimeters (0.47 inches) in the half-burnt areas, and from 30 centimeters (11.8 inches) by 10 millimeters (0.39 inches) to 80 centimeters (31.5 inches) by 22 millimeters (0.87 inches) in the sunny complete burns. The average growth in height at the higher altitudes is 2 centimeters (0.8 inches) per year; at the lower altitudes it is 8 centimeters (3.1 inches) in the complete burns and 5 centimeters (2.0 inches) in the half burns, even with the strong competition of the blueberry cover. The figures obtained for the growth of adult trees in the burn of 1864 are less conclusive, but they show that the rate of growth at 9,000 feet is from two to three times greater than that at 10,500 feet. This is true, however, only for height. The reflection and radiation from the gravel soil are so strong that the lower foot or two of the air has a climate quite its own. The effect of this is strikingly shown in the formation at the base of the tree of a skirt of branches from three to four times longer than those just above. Also the average base diameter of such trees slightly exceeds that of the much taller trees at lower altitudes, but the stem tapers off much more rapidly after the first foot or two.

In determining the age and growth of a large number of trees, opportunity was found for studying the direction of greatest radial growth. In 30 per cent of the stems that were eccentric the maximum radius was toward the south. In 20 per cent the direction of greatest growth was north northeast. The percentage for the other directions represented, namely, north, northwest, north northwest, east, east by south, and south southeast, was nearly uniform. It is evident that no rule can be formulated from these facts, though it is interesting to find the maximum radius so rarely toward the west. From the relation of photosynthesis to light, the more frequent occurrence of the maximum radius toward the south is easily explained. Yet this would seem to demand that the greatest growth should regularly be in this direction, which is far from the case. The most striking cases of unequal growth in diameter are clearly the result of competition, and this is probably also the explanation of practically all the cases observed. No record was kept of the total number of symmetric trunks, but a large number were exactly isodiametric. Perhaps somewhat more than half were slightly irregular, but the unequal growth was conspicuous in a relatively small number.

SUMMARY.

CONE PRODUCTION.

Lodgepole pine can mature cones as early as its fifth year, though cones do not usually appear until the tenth to twelfth year. This determines the length of time during which it is imperative that fire be kept out of reproduction if cones are to be available for reseeding. It also shows the rapidity with which new generations of lodgepoles may be obtained for experiments in improving the quality of wood, increasing the rate of growth, etc.

The number of cones produced depends chiefly upon the density of the individuals as expressed in the competition between them. Apart from competition, those physical factors which control growth, especially of the crown, are of most importance. There is also good evidence that in cone production trees often behave as individuals, since trees of the same age show differences which can not be explained by competition or by physical factors.

SEED PRODUCTION.

There is no fixed relation between the amount of seed and the number of cones. The number of seeds varies with the size of a cone, the number of scales in it, and the age of the tree or branch upon which it is borne, though the present results do not show a constant relation with any one of these factors. With occasional exceptions, the number of seeds rises with the number of scales and the length and diameter. The number of seeds decreases with the age of the tree or branch, at least to the extent that 2-year cones show a smaller average than 4-year ones, and the latter smaller than 8-year ones. This is what should be expected in the normal stand, where the intensity of competition affects both cones and seeds.

OPENING OF CONES.

The great majority of cones in a lodgepole forest open naturally, without the aid of fire. Cones are opened every year, and their seeds released by the action of moisture and heat. The opening of each cone is a gradual process, and only a few seeds are released at a time. In addition, the cones open at very different times. The majority of them open in the first few years after ripening or when they are about 10 years old. A number on each tree remain closed longer, and some of these open each year afterward. This continuous and uneven process of opening has two important results. It means the almost complete consumption of the freed seeds of each year by the animal population of the forest, but it insures, on the other hand, an adequate seed supply whenever a fire makes reproduction possible.

Small cones, if fertile, open as readily as large cones. Trees of the same age and in the same stand may show all the cones open in one case, and all closed in another. Without the action of fire, cones open in consequence of weathering and the solution of the resin which holds the scales together, followed by changes in moisture content, which cause them to bend back. The chief value of fire is in removing the resin and releasing the scales, but it thoroughly dries the scales also. Fire does not seriously impair the germinating power of the seeds in a cone unless the latter is thoroughly charred.

DISTRIBUTION OF CONES AND SEEDS.

Cones are distributed primarily by animals, seeds by the wind. The actual grouping of lodgepole seedlings in a burn is largely the result of the roll of cones and the surface wash of seeds. Owing to its light and soil requirements, the extension of lodgepole, except in connection with burns, is of little practical importance.

Squirrels and chipmunks, and to a less extent birds, seem to be the chief consumers of lodgepole seed, and it is their use of them for food which prevents reproduction in situations otherwise favorable. The great reason why a fire makes adequate reproduction possible is that it drives away the rodents for a number of years and thus saves the freed seeds for germination.

GERMINATION.

Tests made of seeds from the two Forests, Targhee and Holy Cross, gave results so diametrically opposite in most cases as to indicate clearly the impossibility of making general rules which will hold for different regions. The discovery that seeds will germinate after fifty to seventy-five years goes to prove that one important service of a fire is the unlocking of a large number of cones which have hoarded their seeds for years.

RELATION TO LIGHT AND WATER.

The minimum light intensity for lodgepole reproduction is 0.1 of full sunshine. Fair reproduction may occur at 0.2, though it is much inferior to that in full sunshine. The light of a mature forest ranges from 0.12 to 0.05, a sufficient explanation of the entire absence of seedlings.

The maximum water content for lodgepole is 35 per cent in loam and about half as great in sand and gravel. The optimum water content is between 12 and 15 per cent, though it rises to 20 per cent where the decay of the needle cover makes the amount of nonavailable water greater. The minimum may fall below 5 per cent in gravel without injury to the tree, except in decreasing its rate of growth. The behavior of lodgepole pine on the dry hills about Sulphur Springs in Middle Park points strongly to the desirability of using it in afforestation experiments on the Great Plains.

RELATION OF REPRODUCTION TO COMPETITION.

The presence of a well-developed cover either greatly reduces the amount of germination or causes the death of many of the young seedlings through competition. This is especially true of dense carpet-like covers of Vaccinium or Arctostaphylos. When the competition of the cover becomes keen only after the seedlings have a good start its effect is seen in the striking retardation of growth, which averages scarcely half the normal. The question of cover competition is one of great importance for the seedling, and some method of artificial control of the cover must sooner or later be developed.

Proper competition between the trees of a lodgepole forest is essential to the development of the best type for lumber. When the competition passes a certain point its effect is readily seen in the suppression of growth. In natural burns there is no remedy for this except thinning, which has not yet been sufficiently tried to warrant definite conclusions. In cuttings it is a relatively simple matter to determine by experiment the proper grouping of seed trees to insure the right degree of competition. In most cases this will be more readily secured by some method of selection cutting rather than by the strip method.

RELATIVE RATE OF GROWTH.

While lodgepole is inferior in the quality of its wood to two or three of its competitors, its more rapid growth largely offsets this disadvantage. For afforestation of watersheds the ability of lodgepole to grow rapidly is of the greatest importance. There is, moreover, little question that under the same conditions the rate of growth is greater in some individuals than in others, which makes possible the development of a variety with a much more rapid growth than the average lodgepole pine now has.

FUTURE DEVELOPMENT AND TREATMENT OF LODGEPOLE FORESTS.

The future of the lodgepole forests of Estes Park, as well as of the central Rocky Mountain region, depends primarily upon the treatment they receive. Under natural conditions the ascendancy of lodgepole will depend upon the frequence of fires. Within National Forests the outcome will be determined by the fire control and by the amount and kind of treatment given. Given a certain sequence of natural conditions, it is possible to forecast with accuracy the future forest cover of a particular region. On the other hand, if certain definite results are desired, all that is needed is to determine the kind of control necessary and to apply it. The broader results of the present ecological study are indicated in the following paragraphs, which deal with the natural outcome with and without fire, and with the consequences of artificial treatment of various kinds.

Under natural conditions, lodgepole forests will extend themselves whenever fires occur along their edge or near at hand, except where some factor, such as high altitude or excessive water content, prevents. With these exceptions lodgepole shows its ability everywhere in the park to replace mixed forests in which it has had a part, or nearly pure stands of other species in which it is of little importance. This ability rests upon its rapid and thorough seeding and upon its rapidity of growth. The extension of the lodgepole forest is most rapid downward. It takes place readily along the same general level in all directions, but especially in the direction of prevailing winds, hence to the southeast. Movement upward within its proper zone is slow, on account of the difficulty of migration, and as the upper limits of the zone are reached it is still further reduced by the increasing difficulty of establishment. In the State as a whole, the same factors that are controlling in the local habitats are extending the range of the lodgepole, especially to the southward. There is little question that through the agency of fires, naturally or artificially, lodgepole forests can be extended throughout the entire State wherever physical factors are not prohibitive. The burned forests in central Colorado appear as thrifty and as much at home as those in the north, while the outposts that have reached southern Colorado appear to be in equally good condition.

Just as the lodgepole is superior to all its associates in ability to occupy a burned area, so it is inferior to them all in its ability to enter an area already occupied and to establish itself there. This is due chiefly, if not wholly, to the fact that it is unable to reproduce normally even in slight shade, and to reproduce or grow with any success whatever in the shade of a normal forest of itself or of other species. Without the advantage afforded by fires, a lodgepole forest or region would find itself gradually but surely restricted by the ability of all the other conifers to invade it and establish themselves. This is small in the case of the yellow pine and the limber pine. It is marked with the Douglas fir, and particularly with the Engelmann spruce and the alpine fir. The lodgepole zone is thus gradually narrowed above as well as below. This process takes place more rapidly above because gravity aids the migration of the Engelmann spruce and the fir, while it hinders the migration of the Douglas fir into the lodgepole zone. The former are also more tolerant than the latter, and thus enter and grow successfully in light intensities too low for the Douglas fir. While such conditions are practically impossible in nature, it seems certain that in a region without fires lodgepole forests would ultimately be replaced by a mixture of Engelmann spruce and alpine fir, or a forest of the former alone, in the upper part of its zone, and by a forest of Douglas fir, often with some yellow pine or limber pine, in the lower portion. If fire were kept entirely out of the lodgepole areas in the central and southern parts of Colorado, these would disappear to be replaced chiefly by forests of Engelmann spruce. These results will come as a natural consequence of increasing efficiency in preventing and checking fires in the National Forests and adjacent areas. The use of fire as a silvicultural agent of the forester will make it possible to secure whichever result is desired. The artificial treatment of lodgepole forests rests upon the three silvicultural methods, namely, burning, cutting, and planting. Planting has not yet been tried on a scale sufficient to indicate its possibilities or to reveal the difficulties involved. The frequent association of yellow pine and lodgepole, and the success of the latter in such dry upland areas as the sagebrush formation of Middle Park, suggests the lodgepole as the most promising species for afforesting the grass lands of plains and parks between altitudes of 5,000 and 9,000 feet. It is probable that when planting methods have once been developed, burning will be a necessary preliminary to their use.

The value of fire as a silvicultural agent is shown by its effect upon reproduction in the case of natural burns. This effect is fivefold: (1) The opening of closed cones, making a large number of seeds suddenly available; (2) the removal of the cover, thus preventing its competition; (3) the preparation of a favorable seed bed, though this may be little more than the removal of competition; (4) the renewal of proper conditions of sunlight; (5) the removal for a time of the seed-eating population of squirrels, chipmunks, and birds. As has already been pointed out, the first four conditions are often met at the edge of forests and in openings without bringing about reproduction of any value whatever. This is so thoroughly the rule in Estes Park that here at least the real importance of fire seems to lie in the removal of the rodents. Naturally, the appearance of lodgepole over a large area can result only when that area has been freed from other trees, a result possible only through fire or cutting. Since the five results given above appear together as the immediate consequences of a fire, it might seem that nothing is gained by trying to determine their relative importance. An understanding of the critical value of the disappearance of the rodents is indispensable in explaining the kind and amount of reproduction under various conditions, and especially in working out a method of planting.

A cut-over area differs from a burn in practically all of the points indicated. There is little change in the number of closed cones, the competition of the cover remains the same, and the seed bed also in large degree. The light intensity is increased, but it is still much less than full sunshine for the seedlings until they have pushed up above the cover. Some slight change may occur in the rodent population, but this is hardly efficient for the first few years at least. From these facts it is clear that optimum reproduction can rarely take place in cut overs. A comparison with the striking reproduction of burns shows that cut-over areas lack practically everything which makes the burn so favorable to reproduction. This emphasizes what foresters have already learned, that cuttings must be burned as a rule in order to insure good reproduction. Theoretically, the best results will be obtained in pure or nearly pure lodgepole stands by clear cutting of the entire forest, followed by thorough burning. Such a method will be unsatisfactory only when there is danger that a fire may sweep through the young burn forest before it reaches the age of efficient cone production. Such fires involve the loss of several or many years of growth, and we may expect to see preventive measures soon carried to the point where they are practically impossible. Meanwhile the necessary provision against a fire during the reproduction period may be secured by strip cutting or selection cutting, depending upon the structure of the forest and the results to be secured. Selection cutting insures the necessary seed supply against a fire during the reproduction period, and has the further advantage of yielding a more uniform distribution of seeds, as well as that of permitting a more thorough utilization of the ground during each generation. Where fires can be prevented or easily stopped, clean cutting with uniform distribution of the cone-bearing tops is the ideal method, owing to the unique effect of fire upon lodgepole reproduction. Where serious danger from fire exists, the best method will be to approximate clear cutting just as closely as the need of provision against fire during the reproductive period will permit.

The lodgepole forest is the key to the silvicultural treatment of the forests of the eastern Rocky Mountains, especially in Colorado and Wyoming. Its position in a zone between Douglas fir and yellow pine below and Engelmann spruce and alpine fir above gives the forester a peculiar advantage. Its enormous seed production, the power of the seeds to remain viable in the cones for years, its preference for soils of moderate water content, the dependence of reproduction upon sunlight, and its rapid growth are all points of the greatest value in enabling the forester to accomplish his results. And it is by means of fire properly developed into a silvicultural method that the forester will be able to extend or restrict lodgepole reproduction and lodgepole forests at will.

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